

The Genus *Littoraria* Griffith & Pidgeon, 1834 (Gastropoda: Littorinidae) in the Tropical Eastern Pacific

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Abstract. Six species of *Littoraria* Griffith & Pidgeon, 1834, are recognized in the Panamic Province: *L. pintado pullata* (Carpenter, 1864), *L. varia* (Sowerby, 1832), *L. zebra* (Donovan, 1825), *L. variegata* (Souleyet, in Eydoux & Souleyet, 1852) (= *L. fasciata* of authors, not Gray, 1839), *L. rosewateri* new species, and *L. aberrans* (Philippi, 1846). The shell, reproductive anatomy, and radula of each are described and illustrated. Three possible interspecific hybrids are recorded. *Littoraria pintado pullata* occurs on oceanic rocky shores, but the others are found in mangrove habitats. Distribution maps are given.

This diversity of species is much lower than in the Indo-West Pacific, and only *L. pintado* is common to the two provinces. Morphological comparison does not suggest any obvious sister-species pairs on either side of the Isthmus of Panama, supporting the idea that speciation and/or extinction since the formation of the Isthmus has obscured such relationships. Phylogenetic relationships with other members of the genus are discussed.

Comparisons of shell morphology confirm trends previously demonstrated in Indo-West Pacific species: those species zoned at higher levels on mangrove trees have thinner shells and are more variable (or polymorphic) in shell color. Extreme intraspecific variation in radular morphology is described in three of these species. *Littoraria aberrans* is one of only four ovoviviparous species with intracapsular metamorphosis in the Littorinidae.

INTRODUCTION

The genus *Littoraria* Griffith & Pidgeon, 1834, consists of a group of 36 littorinid species. In cladistic analyses of morphological characters, the genus has been clearly recognized by two unreversed synapomorphies (closed prostate gland and lack of mamilliform penial glands) which, while not individually unique within the family, combine to define it as a monophyletic group (Reid, 1986, 1989). Its members are mainly tropical in distribution and, although some of the basal species occur in the ancestral habitat of the upper eulittoral on rocky shores, the majority show a close and often obligate association with mangroves, wood, and salt-marsh vegetation. In early taxonomic works, species in this group were considered difficult to delimit and characterize, since shells often show interspecific similarities and intraspecific variability, and color polymorphism is common. However, anatomical features, particularly of the reproductive tract, are now known to provide consistent and reliable characters for the identification of *Littoraria* species (Reid, 1986).

Littorinid gastropods are intensively studied because of their abundance, accessibility on the shore, and worldwide occurrence. Within this well-known family, *Littoraria* species show several peculiarities which make them of particular interest. Their association with mangrove and other vegetation is shared by only one other littorinid genus (*Mainwaringia* Nevill, 1885), and aspects of their field ecology, diet, and zonation patterns on the trees have been described (e.g., Reid, 1985; Kohlmeyer & Bebout,

1986; Newell & Bärlocher, 1993; Blanco et al., 1995). Living on trees, often above the regular reach of the tide, they show behavioral and reproductive specializations, including vertical migration (Reid, 1984), lunar spawning rhythms (Berry & Chew, 1973; Gallagher & Reid, 1974), and ovoviviparity (Reid, 1986, 1989). Where sympatric *Littoraria* species occupy different vertical zones on the trees, they provide a clear example of the correlation between the architectural defense of shells and the intensity of crushing by aquatic predators such as crabs and fish (Reid, 1984, 1986, 1992; Cook et al., 1985; Borjesson & Szelistowski, 1989). The species that inhabit the highest levels, among the foliage, often show discrete polymorphism (*sensu* Ford, 1945) of shell color; these provide a model system for the study of maintenance and adaptive significance of color polymorphism (Cook, 1983, 1986, 1990, 1992; Hughes & Mather, 1986; Reid, 1986, 1987; Cook & Garbett, 1992).

The systematics of *Littoraria* are now relatively well understood, particularly in the Indo-West Pacific province, where the 20 mangrove-associated species have been the subject of a taxonomic monograph (Reid, 1986). The remaining species are mostly familiar and easily identified (species lists in Reid, 1986, 1989). The principal clades indicated in a phylogenetic analysis of morphological characters have been recognized as subgenera, although the species-level phylogeny is not well resolved (Reid, 1986, 1989). Nevertheless, those species in the tropical Eastern Pacific have been neglected. Since the earliest faunistic studies of the mollusks in this region

(Adams, 1852; Carpenter, 1857b; Mørch, 1860), the three larger mangrove-associated species have been familiar (generally under the names *L. varia*, *L. fasciata*, and *L. zebra*), although only from their distinctive shells. These have been illustrated in the few modern identification guides for mangrove mollusks from the Panamic province (Zilch, 1954; Keen, 1958, 1971; Peña, 1971b; Alamo & Valdivieso, 1987), but shell characters are variable, and some confusion has persisted. At least in Colombia, they are gathered for food, and are of potential commercial importance (Cantera & Contreras, 1978). A fourth mangrove-associated species, the enigmatic *L. aberrans*, was for over a century known only from the shell of the holotype (Philippi, 1846a), until briefly redescribed by Rosewater (1980b). An additional species, hitherto variously classified as *L. pullata*, *L. pintado*, or *L. pintado schmitti*, occurs on the rocky shores of remote oceanic islands and peninsulas; only the shell has been illustrated (Bartsch & Rehder, 1939; Keen, 1958, 1971; Palmer, 1963; Rosewater, 1970), and its relationship to the Indo-West Pacific *L. pintado* has been considered (Reid, 1986). The anatomy of all these *Littoraria* species of the Eastern Pacific has been examined during the course of recent studies of the phylogeny and classification of the genus (Reid, 1986, 1989), and two electron micrographs of their radulae have been made (Rosewater, 1980a, b). However, no comprehensive descriptions have yet been published. Furthermore, the geographical distributions of these species are not known in any detail.

The present study therefore aims to provide full descriptions of the *Littoraria* species of the tropical Eastern Pacific (Panamic) province. Radular characters are shown to be extraordinarily variable within species. The reproductive anatomy of *L. aberrans* is uniquely modified in the genus, and this is one of only four members of the Littorinidae that are ovoviviparous with intracapsular metamorphosis (Reid & Geller, 1997). One new species, hitherto confused with *L. aberrans*, is described. Nomenclatural revision necessitates a change in the name of *L. fasciata*. The limited ecological information is reviewed, and supplemented by field observations. Distribution maps are plotted for each species, and their biogeography and relationships discussed in the context of the geological history of Central America.

MATERIALS AND METHODS

This account is based on examination of all material in the collections of the Natural History Museum, London (BMNH), the National Museum of Natural History, Smithsonian Institution, Washington, D.C. (USNM), the Academy of Natural Sciences of Philadelphia (ANSP), and the Museum of Comparative Zoology, Harvard University (MCZ). Personal collections of all species were made in Costa Rica (1985) and Mexico (1994), and are deposited in BMNH. Additional material was borrowed

from the Los Angeles County Museum of Natural History (LACM) and the California Academy of Sciences (CAS). All available type material was examined.

Shell dimensions were measured with vernier calipers to 0.1 mm. Shell height (H) is the maximum dimension parallel to the axis of coiling, shell breadth (B) the maximum dimension perpendicular to H, and the length of the aperture (LA) the greatest length from the junction of the outer lip with the penultimate whorl to the anterior lip. For the purpose of diagnosis, shell shape was quantified simply as the ratio H/B and H/LA (relative spire height, SH), and the range of these ratios quoted. Protoconch whorls were counted as recommended by Reid (1996). To describe the coiling of the operculum, the opercular ratio was defined as the ratio of two parallel measurements, the diameter of the spiral part divided by the maximum length (Reid, 1996). The relative radular length was the total radular length divided by shell height.

Living animals were relaxed in 7.5% (volume of hydrated crystals to volume of fresh water) magnesium chloride solution. Sperm samples were removed from the seminal vesicles of relaxed, living animals, fixed in 0.5% seawater formalin, examined immediately by light microscopy, and drawn by camera lucida. Animals were fixed in 10% seawater formalin buffered with borax, and stored in 80% ethanol before dissection. For general accounts of the male and female anatomy of *Littoraria*, see Reid (1986). Radulae were cleaned by soaking in a hypochlorite bleaching solution at room temperature for about 5 min, rinsed in distilled water, mounted on a film of polyvinyl acetate glue on glass, allowed to dry in air, and coated with gold and palladium before examination in a scanning electron microscope. Unworn portions of radulae were viewed in three orientations: in standard flat view from vertically above the radula (to show shapes of teeth), at an angle of 45° from the front end of the radula (to show shapes of tooth cusps), and at an angle of 45° from the side of the radula (to show relief). The shape of the rachidian tooth was quantified as the ratio of the total length (in flat view) to the maximum basal width. The "hood" of the rachidian is a sharp flange (presumably an additional cutting edge) anterior to the main cusps of the tooth.

The supraspecific classification employed follows that of Reid (1989).

SYSTEMATIC DESCRIPTIONS

Family LITTORINIDAE Anon., 1834

Genus *Littoraria* Griffith & Pidgeon, 1834

Type species: *Littorina pulchra* "Gray" Sowerby, 1832 [= *Turbo zebra* Donovan, 1825]

Diagnosis: Littorinidae without nodulose shell sculpture, with paucispiral operculum, egg groove of pallial oviduct coiled in a single spiral, salivary glands constricted by nerve ring; defining (but not unique) synapomorphies are

closed prostate gland and absence of mamilliform penial glands (after Reid, 1989).

Subgenus *Protolittoraria* Reid, 1989

Type species: *Turbo pintado* Wood, 1828

Diagnosis: Penis not bifurcate; scattered simple penial glands not forming discrete glandular disc; copulatory bursa opening at posterior end of straight section of pallial oviduct; spawn of cupola capsules sculptured by one concentric ring; hood of rachidian tooth slight or absent; six to eight elongate cusps on outer marginal tooth (diagnosis modified from Reid, 1989).

Littoraria (Protolittoraria) pintado pullata (Carpenter, 1864)

(Figures 1, 2A–C, 3A, 4A, B, 5A–E, 6A)

- Littorina* sp. Carpenter, 1857b: 350 (see Carpenter, 1864a).
Littorina pullata Carpenter, 1864a: 477 (Cape St Lucas [Cape San Lucas, Baja California, Mexico]; lectotype (here designated, 11.3 mm, Figure 1B) USNM 12661, seen; 2 paralectotypes USNM 635481, seen; 7 paralectotypes BMNH 1865.12.6.69, seen; 3 paralectotypes BMNH 1968357, seen; 3 paralectotypes ANSP 18627, seen). Carpenter, 1864b: 546, 618. Weinkauff, 1882: 106.
Littorina (Melaraphe) pullata—Keep & Baily, 1935: 199.
Littorina (Melaraphe) scutulata pullata—Burch, 1945: 12. Palmer, 1958: 159.
Littorina pullata—Keen, 1958: 282; fig. 177. Palmer, 1963: 335–336; pl. 61, fig. 6. Keen, 1971: 366; fig. 186. Abbott, 1974: 69.
Littorina (Littoraria) pullata—Rosewater, 1970: 423, 447.
Littoraria pintado pullata—Reid, 1996: 11.
Littorina (Melaraphe) scutulata—Tryon, 1887: 250; pl. 45, fig. 3 (in part, includes *Littorina scutulata* and *Littorina plena*; not Gould, 1849).
Littorina scutulata—Abbott, 1974: 67–68 (in part, includes *Littorina scutulata* and *Littorina plena*; not Gould, 1849).
Littorina schmitti Bartsch & Rehder, 1939: 9–10; pl. 2, fig. 4 (shore south of landing, Clipperton Island; holotype USNM 472547, Figure 1F; seen). Keen, 1971: 366; fig. 187.
Littorina (Littoraria) pintado schmitti—Rosewater, 1970: 423, 449–450; pl. 346, figs 13–16.
Littoraria (Littoraria) pintado—Reid, 1986: 64, 73 (not *Turbo pintado* Wood, 1828, which is the nominate subspecies).
Littoraria (Protolittoraria) pintado—Reid, 1989: 96 (not Wood, 1828).

Taxonomic history: Despite an adequate initial description (Carpenter, 1864a), this subspecies has long remained misunderstood and poorly known. Following Tryon (1887), it has often been considered a color form or subspecies of *Littorina scutulata* (Burch, 1945; Palmer, 1958; Abbott, 1974; see Reid, 1996). Bartsch & Rehder (1939) gave the name *Littorina schmitti* to examples from Clipperton Island, and noted a relationship to "*Littorina*"

pintado from the Indo-West Pacific. However, the conspecificity of Mexican specimens with those from Clipperton Island, and with *Littoraria pintado*, was only pointed out much later (Reid, 1986).

Diagnosis: Shell smooth with fine incised spiral lines, brown to black, often with pale flecks and spiral lines, aperture brown, columellar pillar white. Penis long, simple, no glandular structures visible externally.

Shell (Figure 1): Mature shell height 5–16.9 mm. Shape high-turbinate to elongate ($H/B = 1.47$ – 1.71 , $SH = 1.47$ – 2.02); spire whorls only slightly rounded, sutures slightly impressed; indistinct angulation at periphery of last whorl; of moderate thickness. Mature lip not flared; columellar pillar long, straight and somewhat flattened, only slightly hollowed at base. Sculpture smooth except for fine incised spiral lines over whole surface, 8–13 above periphery of last whorl, but often indistinct or obsolete; entire surface with fine spiral microstriae if well preserved; no discernible periostracum. Protoconch 0.30 mm diameter, about 3.5 whorls, terminated by sinusigera rib, sculpture not preserved. Color: densely pigmented, largely obscuring pale ground color; effect is chocolate brown to black with variable patterning of pale grey to white: finely flecked, marbled or tessellated, alternatively with narrow spiral lines (2–17 on last whorl), or combination of flecks and lines; pale patterning usually stronger on base and from shoulder to suture; shell rarely almost entirely black. Columellar pillar white, edged with chocolate brown; interior blackish brown with pale lines showing through.

Animal: Head, tentacles, and sides of foot dark grey to black, sometimes a pale stripe behind eye and pale spot at inside of tentacle base. Opercular ratio 0.31–0.36. Penis (Figure 2A–C) long, vermiform, tapering only near tip; fine annular wrinkles extend almost to tip, so that filament is not differentiated from base; base not bifurcate, no glandular disc visible externally, but base probably contains simple subepithelial glandular cells (as confirmed by histological examination of nominate subspecies, Reid, 1989); sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; unpigmented except for small grey or blackish area at very base. Euspermatozoa 107–114 μm ; paraspermatozoa (Figure 3A) spherical to oval, maximum diameter 15–22 μm , packed with large spherical granules (to 6 μm diameter), single rod-pieces small and often irregular (6–14 μm long). Pallial oviduct (Figure 4A, B) with spiral section of 3.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) about two-thirds of a whorl; bursa small, at posterior end of straight section of pallial oviduct. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule (pelagic cupola capsule with single annular ridge and single ovum described in nominate subspecies;

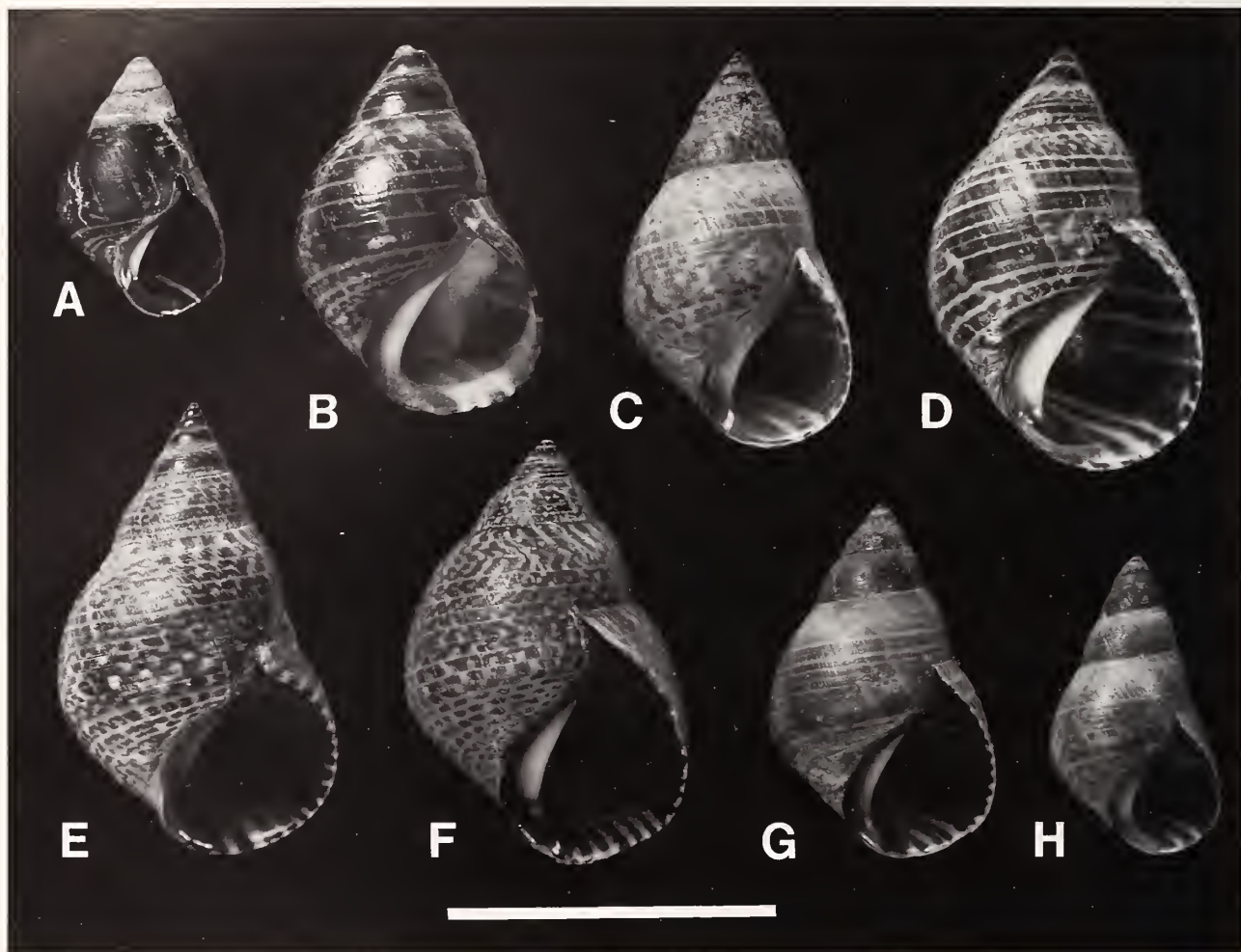
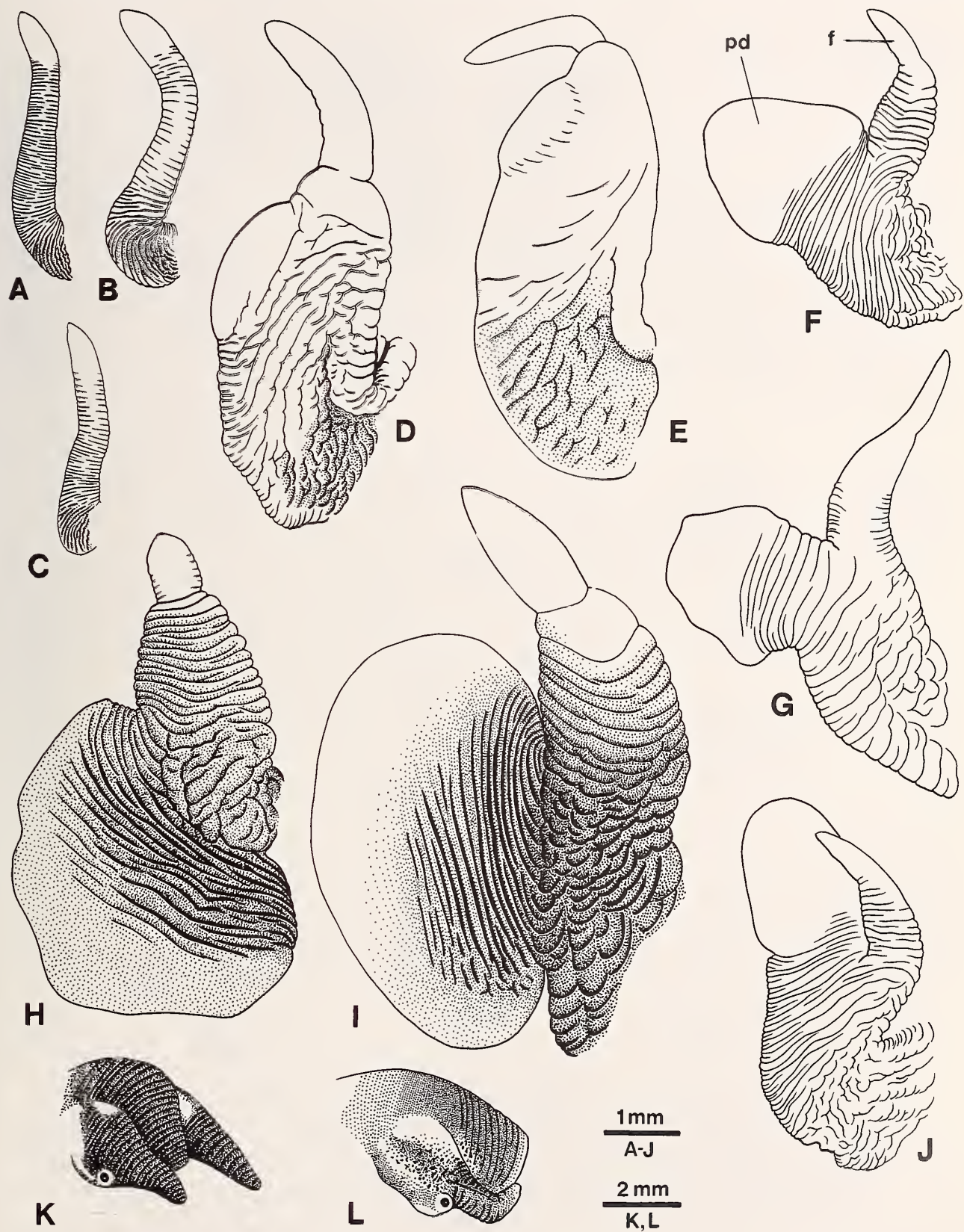


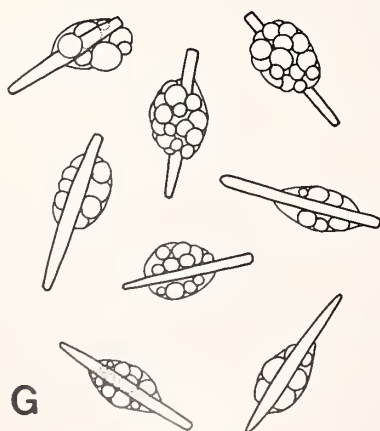
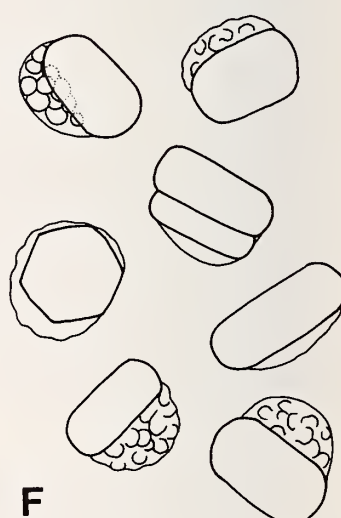
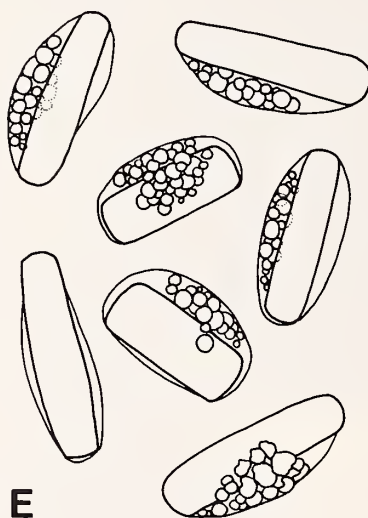
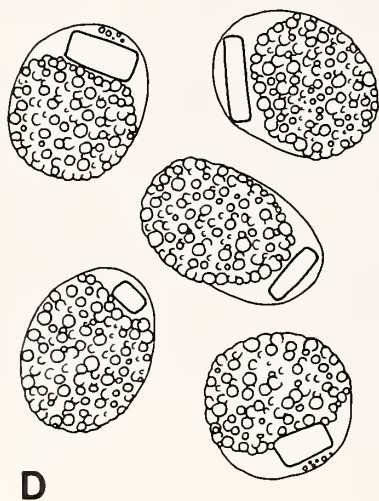
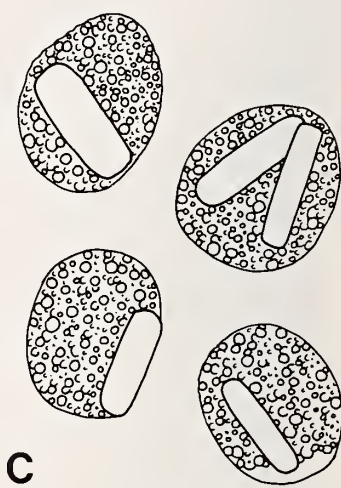
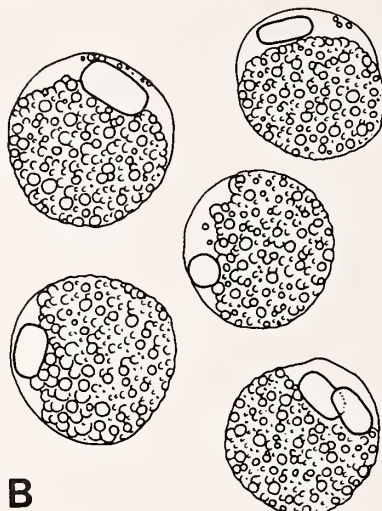
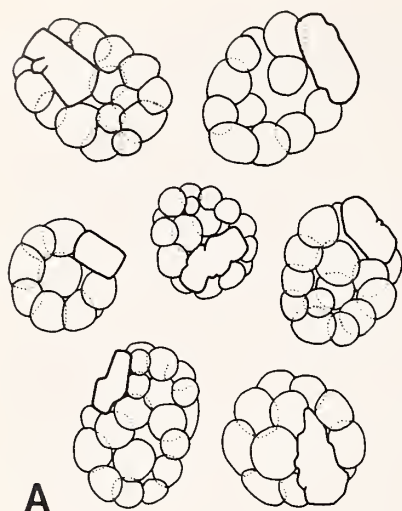
Figure 1

Shells of *Littoraria pintado pullata*. A. Bahía Santa María, Baja California, Mexico (BMNH 1996198; small, black shell form from algal pools at top of eulittoral zone). B. Lectotype of *Littorina pullata* Carpenter, 1864 (USNM 12661); Cabo San Lucas, Baja California, Mexico. C. Socorro Island, Mexico (CAS 96233). D. Cabo San Lucas, Baja California, Mexico (BMNH 1996199). E. Punta Arena, Cerralvo Island, Gulf of California, Mexico (CAS 107727). F. Holotype of *Littorina schmitti* Bartsch & Rehder, 1939 (USNM 472547); Clipperton Island. G. Cabo San Lucas, Baja California, Mexico (BMNH 1996199). H. María Madre Island, Tres Marias Islands, Mexico (CAS 32564). Scale bar = 10 mm.

Figure 2

Penes and heads of *Littoraria pintado pullata* (A–C), *L. variegata* (D, E, L), *L. varia* (F, G, J, K) and *L. zebra* (H, I). A–C. Penes of *L. pintado pullata*. A, B. Cabo San Lucas, Baja California, Mexico (BMNH 1996209; shell H of A = 9.7 mm, shell H of B = 10.4 mm). C. Bahía Santa María, Baja California, Mexico (BMNH 1996210; shell H = 7.1 mm). D, E. Penes of *L. variegata*. D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211; shell H = 20.3 mm). E. Topolobampo, Sinaloa, Mexico (BMNH 1996212; shell H = 15.9 mm). F, G. Penes of *L. varia*. F. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; shell H = 19.5 mm). G. Panama (BMNH 1867.5.22.27; shell H = 28.9 mm). H, I. Penes of *L. zebra*. H. Golfito, Costa Rica (BMNH 1996214; shell H = 26.8 mm). I. Puntarenas, Costa Rica (BMNH 1996215; shell H = 29.8 mm). J. Penis of *L. varia*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; shell H = 19.1 mm). K. Head of *L. varia*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213). L. Head of *L. variegata*; Topolobampo, Sinaloa, Mexico (BMNH 1996212). Abbreviations: f, penial filament; pd, penial glandular disc.





20 μ m

Struhsaker, 1966); type of protoconch indicates planktonic development.

Radula (Figure 5A–E): Relative radular length 1.46–4.09. Rachidian: length/width 0.92–1.37; cusps variable: central cusp pointed (Figure 5D), elongate leaf-shaped (Figure 5E) or very elongate with rounded tip (Figure 5B); smaller pointed cusp and outer denticle on either side; hood developed only as small ridge (Figure 5C–E), or sometimes absent (Figure 5A, B). Lateral: five to six cusps, largest central cusp elongate, but variable in shape (pointed, leaf-shaped or bluntly rounded); two small pointed cusps on inside and two to three on outside of main cusp. Inner marginal: four cusps, largest central cusp shaped like that on lateral; two smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: six to eight elongate pointed cusps, outermost largest. See Remarks.

Material examined: Types as indicated; 26 lots; two protoconchs; nine penes; two sperm samples; six pallial oviducts; eight radulae. (Of nominate subspecies: lectotype of *Turbo pintado* Wood, 1828, BMNH 1968368; 50 lots; one protoconch; seven penes; three sperm samples; four pallial oviducts; three radulae).

Habitat: On rock (including granite, beachrock, and concrete) in uppermost eulittoral and low littoral fringe, clustered in crevices and on sides of rocks; at one locality (Bahía Santa María, NE of Cabo San Lucas, Baja California) submerged or clustered at margins of small algal pools at top of shore; usually on strongly wave-exposed shores. Occurs only at sites with clear, oceanic water. Abundant only at tip of Baja California and on oceanic islands (e.g., 5375 per m² at Socorro Island (Mille-Pagaza et al., 1994).

Range (Figure 6A): Southern Baja California from Todos Santos (BMNH) to 35 km N of La Paz (24°21'N; BMNH; but common only close to Cabo San Lucas); Clarion Island and Socorro Island in the Revillagigedo Islands (CAS, LACM); Tres Marias Islands (CAS); Clipperton Island (USNM). There is also a single collection of four specimens from Cocos Island (5°33'N, LACM) much farther to the southeast; since this species is characteristically found on oceanic islands, this record is

probably reliable. Only occasional specimens have been found on the mainland of Mexico, e.g., 25 km SW Puerto Vallarta (BMNH), 10 km N of Melaque (18°48'N; BMNH), and recorded from Mazatlán (Carpenter, 1857b, 1864a). Records from the state of California (e.g., Burch, 1945; Abbott, 1974) are believed to be misidentifications of *Littorina scutulata* and/or *Littorina plena* Gould, 1849, as in one lot in CAS.

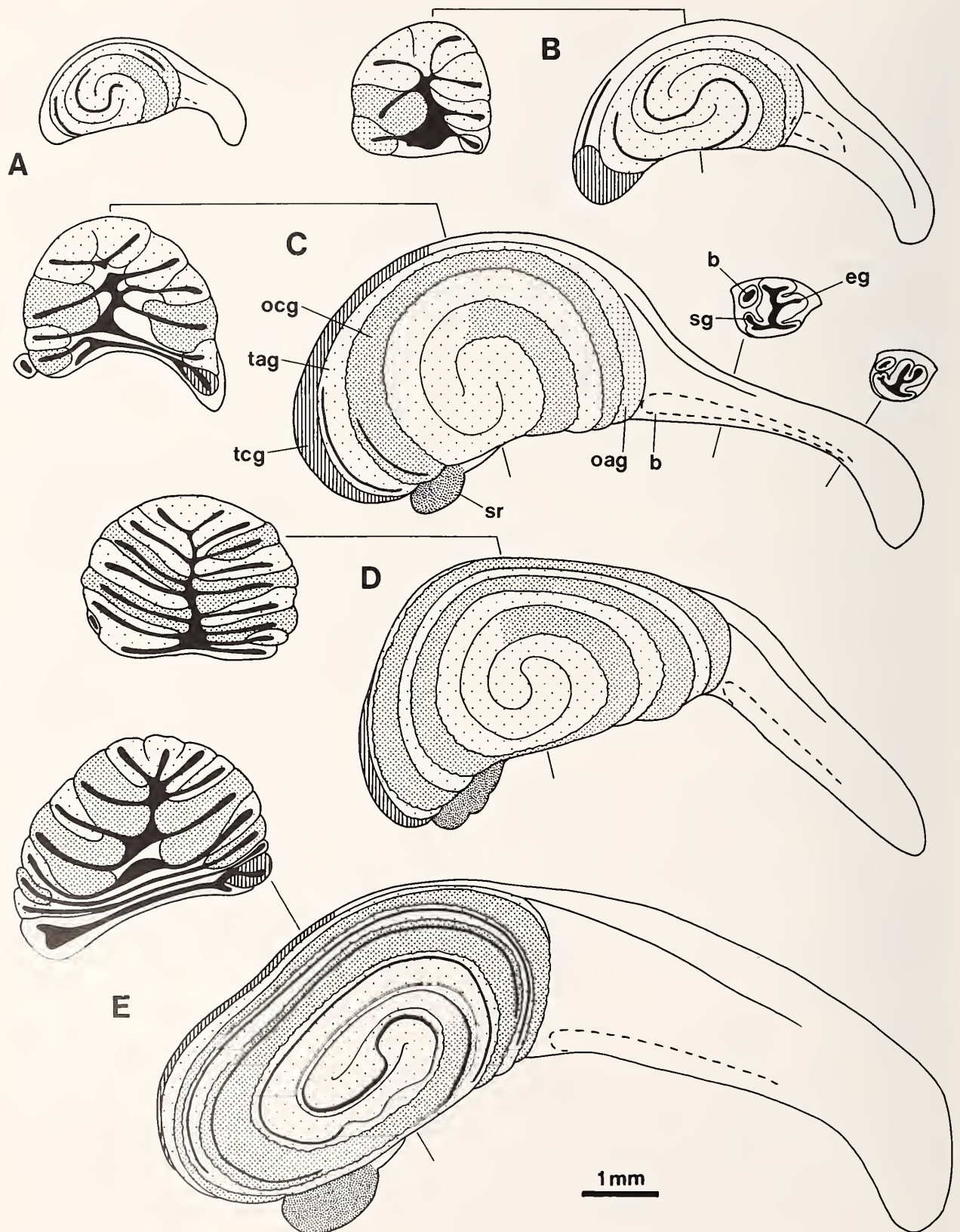
Remarks: The nominate subspecies, *L. pintado pintado*, has a very wide distribution in the Indo-West Pacific; this range is disjunct, with one area in the south and western Indian Ocean (southeast Africa, Madagascar, Mascarene Islands, Somalia) and another in the northern and western Pacific (Ryukyu, Bonin, Caroline, Mariana, Marshall, and Hawaiian Islands) (Rosewater, 1970; Reid, 1986). Although the two areas of occurrence are separated by about 8000 km, no consistent morphological differences in shells, anatomy, or radulae have been detected (personal observation).

The Eastern Pacific records of *L. pintado pullata* are at least 4500 km from the closest known occurrence of the nominate subspecies in the Indo-West Pacific, in the Hawaiian Islands. The close relationship between Eastern Pacific and Indo-West Pacific forms was first noted by Bartsch & Rehder (1939) when they described shells from Clipperton Islands as a new species, *schmitti*, although they did not mention *pullata*. Curiously, Rosewater (1970) reduced *schmitti* to a subspecies of *pintado*, while remarking that *pullata* was an “apparent analogue” of *pintado* in the Eastern Pacific. Reid (1986) found no differences in the reproductive anatomy of *pullata* and *pintado*, and synonymized all three names. This has been confirmed in the present study of additional material, which has included examination of sperm and radulae. However, there are consistent differences in shell coloration. Since all known species of *Littoraria* differ from each other in penial shape (Reid, 1986), separation at specific level does not seem warranted at present. The category of subspecies is appropriate for such a case of minor differentiation combined with allopatric distribution, and carries the implication that although the differentiation probably reflects genetic isolation, there is no morphological evidence for reproductive isolation. In the

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Figure 3

Paraspermatozoa of *Littoraria pintado pullata* (A), *L. varia* (B, C), *L. zebra* (D), *L. variegata* (E, F), *L. rosewateri* Reid, sp. nov. (G, H) and *L. aberrans* (I). A. Cabo San Lucas, Baja California, Mexico (BMNH 1996209). B. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213). C. Estero Aguadulce, Bahía Parita, Panama (USNM 733057; alcohol preserved). D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996216). E. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211). F. Estero Aguadulce, Bahía Parita, Panama (USNM 733055; alcohol preserved, therefore granules indistinct). G, H. Golfito, Costa Rica (BMNH 1996217). I. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). All samples from single individuals; unless otherwise noted, all samples fixed in 0.5% seawater formalin.



nominate subspecies, coloration is predominantly white to pale grey, with spiral rows of small black or brown spots or flecks (18–40 rows on final whorl); although the spotting may occasionally be quite dense, the spots do not fuse to form spiral bands. In contrast, in *L. pintado pullata* the predominant coloration is black to brown, and in addition to varying degrees of pale spotting or marbling, most specimens show white spiral lines.

The geographical distribution of *L. pintado* is of particular interest, since it is one of the few molluscan species, and the only littorinid, to span both Indo-West Pacific and Eastern Pacific provinces. These zoogeographic regions are separated by “Ekman’s Barrier,” a 5000 km expanse of deep ocean without island stepping stones, which appears to have acted as an effective barrier for most shallow-water benthic invertebrates (Vermeij, 1987; Richmond, 1990). However, the barrier is not complete; although almost no Panamic mollusks are known from the Indo-West Pacific, a small number of typically Indo-West Pacific species have been recorded in the Eastern Pacific. The most recent compilation of these listed 61 prosobranch gastropods, of which 56% are found only on the oceanic islands off the American mainland (Emerson, 1991). The rarity of most of these species, combined with their absence from the limited fossil record of western Central America, suggests that the majority are recent (post-Pliocene) arrivals derived by dispersal from the Central Pacific, and that many of the species may be unable to maintain viable populations without replenishment from the source areas to the west (Emerson, 1991). Eastward dispersal is believed to take place mainly by larval transport in the North Equatorial Countercurrent, in which drifter buoys have covered the distance from the Line Islands to the Eastern Pacific in as little as 100 days (Richmond, 1990). Most of the Indo-West Pacific immigrants, particularly the tonnoideans, are known to possess long-lived (teleplanic) larvae able to survive in the plankton for this length of time (Scheltema, 1988). During the periodic El Niño events which considerably alter oceanographic patterns in the Central and Eastern Pacific, this passage may be accomplished in half the time, but the main source area is still considered to be in the Line Islands, lying in the eastward flow of the North Equatorial

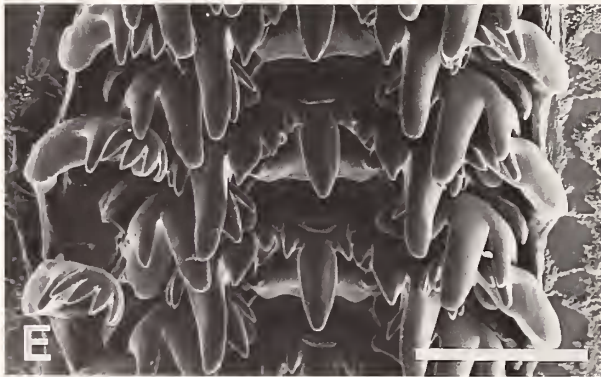
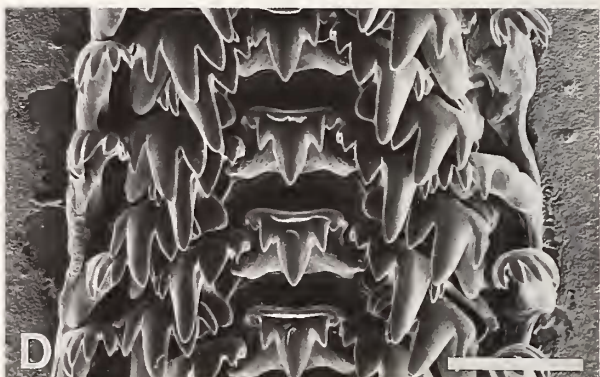
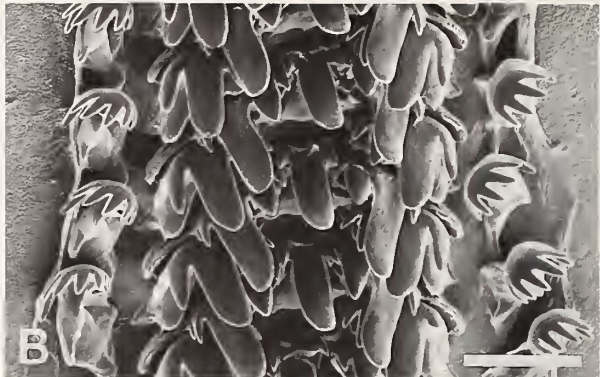
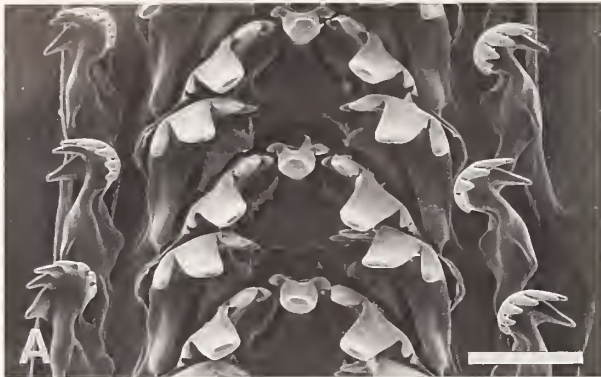
Countercurrent (Richmond, 1990). The evolutionary consequences of trans-Pacific dispersal appear to have been limited. For ecological reasons, some arrivals in the Eastern Pacific may be unable to maintain viable populations there. In those that do, trans-Pacific dispersal is apparently frequent enough to prevent isolation and genetic divergence in the Eastern Pacific; among gastropods, only four Eastern Pacific species or subspecies (excluding *L. pintado pullata*) were interpreted as endemic derivatives of recent immigrants from the Indo-West Pacific by Vermeij (1990).

In many respects, however, *L. pintado* does not conform to the distributional and developmental characteristics shown by other gastropods with trans-Pacific distributions. Quite clearly, *L. pintado pullata* maintains viable populations in the Eastern Pacific, at least in Baja California and on the oceanic islands where it is abundant. Indeed, throughout the range of the species as a whole, it seems to be found largely on oceanic islands, and this habitat specialization explains its almost complete absence from the mainland of Mexico and Central America. Whether the island populations are in genetic contact is unknown, but surface current patterns (Wyrtki, 1965) suggest that this is possible. During the period May to December, the strong North Equatorial Countercurrent could perhaps transport egg capsules and larvae from Clipperton Island to Cocos Island to the east, sweeping northwestward parallel with the Mexican coast toward the Revillagigedo Islands. During the winter this current disappears, while from February to June the California Current flows south and southeast, turning westward to join the North Equatorial Current, thus potentially connecting the populations of Baja California, the Revillagigedo Islands, and Clipperton Island. The spawning season in the Eastern Pacific is unknown, but in Hawaii *L. pintado pintado* produces egg capsules all year round (Struhsaker, 1966). The length of larval life has not been recorded; when reared in the laboratory in Hawaii, veligers survived for 11 days from the time of spawning (Struhsaker, 1966). In a littorinid species with a similar protoconch, *Nodilittorina hawaiiensis* Rosewater & Kadolsky, 1981, the total time to larval settlement in the laboratory was 3–4 weeks (Struhsaker & Costlow, 1968, as *Littorina pic-*

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Figure 4

Pallial oviducts of *Littoraria pintado pullata* (A, B), *L. varia* (C), *L. variegata* (D) and *L. zebra* (E). A. Bahía Santa María, Baja California, Mexico (BMNH 1996210; shell H = 8.8 mm). B. Cabo San Lucas, Baja California, Mexico (BMNH 1996209; shell H = 12.6 mm). C. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; shell H = 25.2 mm). D. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211; shell H = 22.0 mm). E. Golfoito, Costa Rica (BMNH 1996214; shell H = 27.0 mm). Transverse sections taken at levels indicated, viewed from anterior (i.e., right side of figure). Abbreviations: b, copulatory bursa (dashed line; visible only by dissection); eg, egg groove (visible externally if darkly pigmented, as in E, then indicated by thick line); oag, opaque albumen gland (light stipple); ocg, opaque capsule gland (dark stipple); sg, sperm groove (leading ventrally to seminal receptacle); sr, seminal receptacle (darkest stipple); tag, translucent albumen gland (lightest stipple); tcg, translucent capsule gland (cross-hatched); in sections, spiral lumen is black.



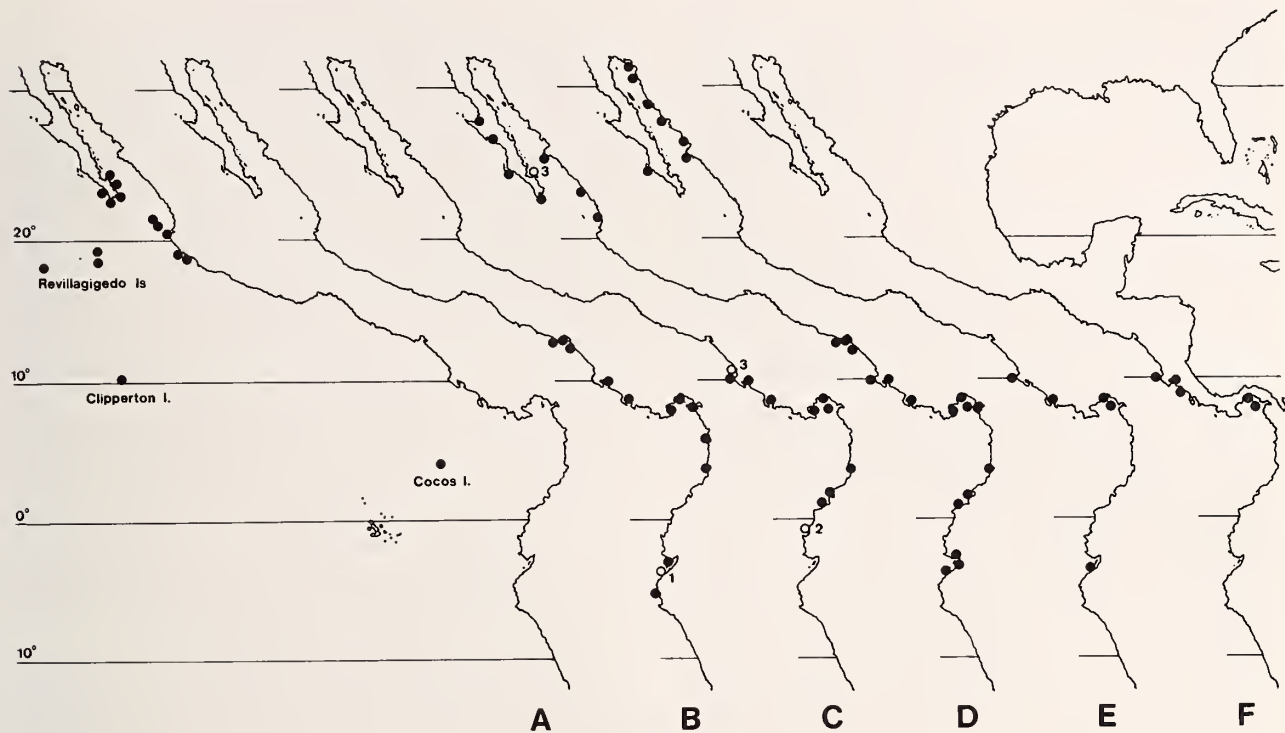


Figure 6

Distribution maps of six Eastern Pacific *Littoraria* species. A. *L. pintado pullata*. B. *L. varia*. C. *L. zebra*. D. *L. variegata*. E. *L. rosewateri* Reid, sp. nov. F. *L. aberrans*. Key: closed circles, material examined; open circles, records from literature (1, Peña, 1970, 1971b; 2, Guerrini, 1990; 3, Pilsbry & Lowe, 1932).

ta). This is sufficient to permit transport for approximately 1000 km at some of the faster average current flows suggested by Wyrki (1965), but is much shorter than the developmental times of long-lived teleplanic larvae (Scheltema, 1988). Larval dispersal between the more distant islands is therefore unlikely to be frequent in normal seasons, but might take place under the exceptional conditions of El Niño events (Richmond, 1990). *Littoraria pintado pullata* is notably absent from the Galápagos Islands (Finet, 1994) which, although only 750 km from Cocos Island, lie outside the path of the North Equatorial Countercurrent (Finet, 1991). Another peculiarity of *L. pintado* in this context is that it is distributed in the

northern Central Pacific (Rosewater, 1970; personal observation of museum collections), the closest occurrence to the Eastern Pacific being in the Hawaiian Islands. In comparison, all but one of the other 60 trans-Pacific prosobranchs listed by Emerson (1991) occur in the Line Islands and/or French Polynesia (although many do in addition occur in the Hawaiian Islands). Since the Hawaiian Islands are so distant (about 4500 km) from the range of *L. pintado pullata*, and furthermore lie in the weak westward-flowing North Equatorial Current (McNally et al., 1983), it is improbable that there is any gene flow between the populations in the Indo-West Pacific and the Eastern Pacific, even during the exceptional El Niño

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Figure 5

Radulae of *Littoraria pintado pullata* (A–E) and *L. variegata* (F–H). A, B. Cabo San Lucas, Baja California, Mexico (BMNH 1996209; two views of radula, flat and at 45°; shell H = 10.4 mm). C, D. Bahía Santa María, Baja California, Mexico (BMNH 1996210; two views of radula, flat and at 45°; shell H = 8.8 mm; small, black shell form from algal pools at top of eulittoral zone). E. Bahía Santa María, Baja California, Mexico (BMNH 1996210; at 45°; shell H = 8.7 mm; normal shell form from open rock surfaces). F. Topolobampo, Sinaloa, Mexico (BMNH 1996212; at 45°; shell H = 15.9 mm). G, H. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996211; two views of radula, flat and at 45°; shell H = 20.3 mm). Abbreviation: h, “hood” of rachidian tooth. Scale bars = 50 µm.

events (Richmond, 1990). This likely genetic isolation may be reflected by the consistent differences in the shell pigmentation of the two, and these arguments support the assertion that *L. pintado pullata* should be recognized at least as a distinct subspecies. Information on the genetic interrelationships of *L. pintado* throughout its range would be most desirable.

Unfortunately, littorinids of high-energy rocky shores are seldom preserved as fossils, and the marine Tertiary record of western Central America is poor, so that there is no fossil evidence for the history of *L. pintado* in the Eastern Pacific. Nevertheless, the evidence reviewed above does suggest that *L. pintado* is not in the same category as those other non-tonnoidean gastropods with trans-Pacific distributions, which have been interpreted as recent colonizers, sometimes tenuously established, which have in general not differentiated from their parent populations in the Central Pacific (Vermeij, 1987, 1990; Emerson, 1991). Instead, *L. pintado pullata* can be added to the four possible examples of Eastern Pacific endemic gastropods derived from Indo-West Pacific immigrants (listed by Vermeij, 1990). The origin of *L. pintado pullata* is still likely to have been relatively recent in geological terms, since the islands on which it occurs are all of Pleistocene age, and elsewhere in the Eastern Pacific only the Galápagos are older (Emerson, 1978). Although dispersal from the Hawaiian Islands to the Eastern Pacific appears to be unlikely under present conditions, *L. pintado* may have been more widely distributed in the Central Pacific in the past. For example, during the sea level fluctuations of the Pleistocene, suitable habitat (high oceanic islands lacking well-developed reefs) may have been more widespread. An alternative scenario, not requiring dispersal across the Pacific, is that the distribution of *L. pintado* is an ancient one, predating the Miocene division of the Tethys Sea and the Pliocene formation of the Isthmus of Panama. This is not credible, in view of the geological ages of the Eastern Pacific islands. Furthermore, the morphological identity of the two subspecies is unlikely to have been maintained if they have been separated since vicariance of an ancient Tethyan distribution. Once again, genetic evidence will be valuable in testing this assertion.

Morphologically, this species is of interest as it shows a number of features suggesting that it is the basal branch within the clade *Littoraria* (phylogenetic analyses by Reid, 1986, 1989). These include the cupola-type egg capsule (biconvex elsewhere in the genus), lack of a discrete penial glandular disc, and the poorly developed or absent hood on the rachidian radular tooth (hitherto recorded only as absent; Reid, 1986, 1989). If correct, this implies that *L. pintado* (or the clade of which it is the only surviving member) is at least as old as any other *Littoraria* species. Other members of this genus are recorded from the Lower Eocene (Reid, 1989). This does not, however, affect the biogeographic scenarios dis-

cussed above, which depend upon the age of the separation of the two subspecies, and not on that of the clade.

Radular variation is striking in this species. Five specimens from Bahía Santa María, Baja California, suggest a possible correlation with shell form or habitat. Two examples of a peculiar small (< 8.8 mm) almost black shell form, with eroded spire, collected from the unusual habitat of algal pools high on the shore (Figure 1A), showed radulae with relatively smaller and more pointed major cusps, and more well developed rachidian hood (Figure 5C, D). Three shells of typical form (7.2–14.7 mm), collected on open rock surfaces at the same locality (similar to Figure 1D), showed radulae with more elongate cusps and only slightly hooded rachidian (Figure 5E); these were similar to examples from Cabo San Lucas (Figure 5A, B), and to specimens of *L. pintado pintado* from Hawaii and Mauritius. No other anatomical differences were detected among specimens from Bahía Santa María. Further investigation is required, but a possible explanation of these preliminary observations is an ecophenotypic effect on radular tooth shape, as has recently been demonstrated in the littorinid *Lacuna* (Padilla, 1998).

This species is common only near Cabo San Lucas and on the relatively inaccessible offshore islands, which explains why it has remained poorly known, and has seldom been figured or described. Among other littorinids in the Panamic province, confusion is possible with *Nodilittorina* species such as *N. aspera* (Philippi, 1846) and *N. penicillata* (Carpenter, 1864); these shells are separated by their entirely brown columella and more pronounced oblique axial stripes of black and white; anatomically, *Nodilittorina* species have a bifurcate penis with a glandular disc and single mamilliform gland, and a pallial oviduct with single loop in the albumen gland only (Reid, 1989). In the Californian province, *Littorina scutulata* and *Littorina plena* are similar in shell outline, but generally show coarser tessellation and lack spiral lines except on the base; their penes have glandular protrusions and there are three consecutive spiral loops in the pallial oviduct (Reid, 1996). The distinction from the nominate subspecies in the Indo-West Pacific has been described earlier.

Subgenus *Littoraria* Griffith & Pidgeon, 1834

Diagnosis: Penis usually bifurcate, with differentiated penial glandular disc; paraspermatozoa lacking pseudotrich (Healy & Jamieson, 1993; "flagellum" of Reid, 1986, 1989); spawn of biconvex discoidal capsules; rachidian tooth usually hooded (diagnosis modified from Reid, 1989). Note that phylogenetic analysis of Reid (1989) suggested this is a paraphyletic or polyphyletic assemblage.

Littoraria (*Littoraria*) *varia* (G.B. Sowerby, 1832) (Figures 2F, G, J, K, 3B, C, 4C, 6B, 7A–C, 8A–E)

Littorina varia G.B. Sowerby, 1832: part 37; pl. 211, fig. 4
(Panama; lectotype (here designated) Sowerby, 1832:

- pl. 211, fig. 4). Adams, 1852: 400–401. Souleyet, in Eydoux & Souleyet, 1852: 561; atlas pl. 31, figs 43–45 (as “*Littorina costulée*” in caption). Reeve, 1857: *Littorina* sp. 19; pl. 4, fig. 19a, b. Mörch, 1860: 69. Dall, 1909: 231, 285 (in part, includes *Littoraria variegata*). Keen, 1958: 282; fig. 178. Keen, 1971: 366; fig. 188. Peña, 1971b: 47. Rosewater, 1980a: 5; figs 3, 4 (radula). Guerrini, 1990: 14.
- Littorina varia*—Philippi, 1846b: 2: 99–100; *Littorina* pl. 1, figs 2, 3. Weinkauff, 1882: 53; pl. 6, figs 14, 15.
- Littorina (Melaraphe) varia*—Tryon, 1887: 246; pl. 43, fig. 44 (in part, includes *Littoraria variegata*).
- Littorina (Littorinopsis) varia*—von Martens, 1900: 580. Rosewater, 1970: 423. Alamo & Valdivieso, 1987: 25; fig. 38.
- Littorina (Algaroda) varia*—Zilch, 1954: 81; pl. 3, fig. 8.
- Littoraria (Littoraria) varia*—Reid, 1986: 73; figs 4j (penis), 18 (cladogram). Reid, 1989: 97.
- ?*Littorina perdix* King & Broderip, 1832: 345 (no locality; types lost).
- Littorina costulata* ‘Souleyet’ Tryon, 1887: 246, 292 (*nomen nudum*).
- Littorina (Littorinopsis) fasciata*—Abbott, 1974: 69; pl. 3, fig. 567 (in part; includes *Littoraria variegata*; not Gray, 1839 = *Littoraria zebra*).

Taxonomic history: No type specimens are known to exist and a lectotype figure is here designated. Nevertheless, there is no uncertainty about the identity of this taxon, and the name *varia* has been employed by most authors, in various generic combinations, throughout its history. Tryon (1887) and Dall (1909) had a broader concept of this taxon, including *L. variegata*. The identity of *Littorina perdix* King & Broderip, 1832, is uncertain; no original material has been located in BMNH. The original diagnosis was inadequate, but the dimensions given (equivalent to 20.6×13.5 mm), together with the raised spiral striae, and white aperture with brown-spotted margin, support its synonymy with *L. varia*, and preclude all other South American littorinids. No locality was given; the title of the paper suggests that all specimens were collected on the South American voyages of the *Adventure* and *Beagle* between 1826 and 1830, neither of which visited the geographical range of *L. varia* (King, 1839). Nevertheless, in the same paper some species were also described from the Cuming and Sowerby collections, from localities such as Lima and Panama, which were not visited during these voyages. The identity of *Littorina perdix* with *L. varia* is therefore a possibility.

Diagnosis: Shell thick-walled; sculpture of strong spiral ribs; color whitish with minute brown flecks, aperture and columella white. Penis with small filament, large glandular disc on branch of base, unpigmented.

Shell (Figure 7A–C): Mature shell height 16–34.4 mm. Shape high-turbinate (H/B = 1.41–1.53, SH = 1.51–1.65); spire whorls only slightly rounded, sutures slightly channelled; angulation at periphery of last whorl marked by largest rib; thick-walled. Mature lip not flared; columella broad and hollowed. Sculpture of strong spiral ribs,

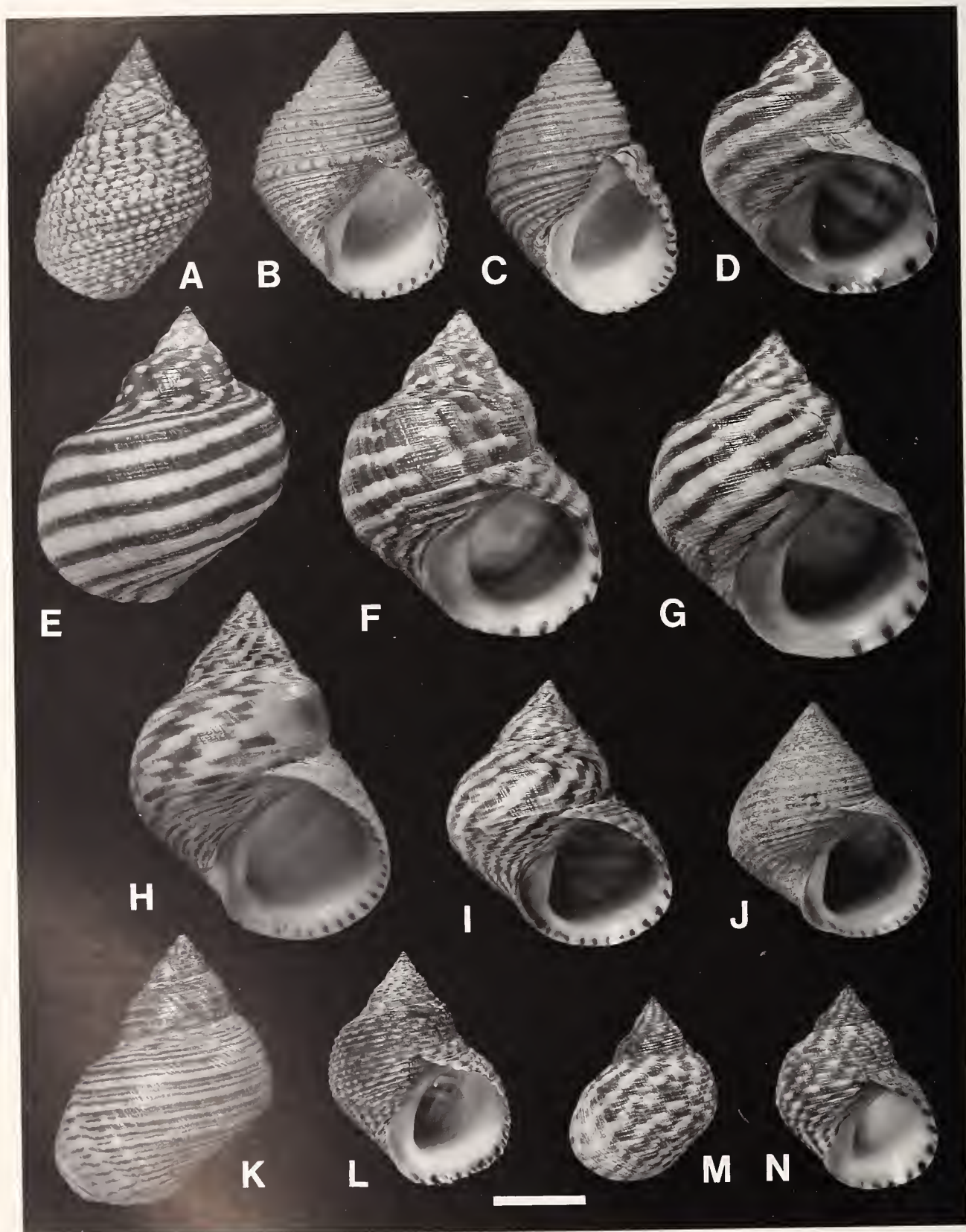
about 12–16 on last whorl, with one to two smaller cords in the broad spaces between each; axial growth lines distinct, especially near end of last whorl, giving slightly cancellate appearance between ribs; surface shiny, with only faint spiral microstriae; no discernible periostracum. Protoconch 0.31 mm diameter, about three whorls, terminated by sinusigera rib, sculpture not preserved. Color whitish to cream, closely and minutely flecked with dark brown; pattern sometimes aligned near suture to form close, narrow, axial stripes; pattern occasionally faint or absent. Columella and interior of aperture white; apertural margin marked with dark brown spots where pattern shows through.

Animal: Head, tentacles and sides of foot black; unpigmented stripe behind eye (Figure 2K). Opercular ratio 0.33–0.40. Hypobranchial gland exceptionally large, up to 3.0 mm wide in shell of 25.3 mm. Penis (Figure 2F, G, J) with large, wrinkled base and small smooth filament (15–20% total length); base bifurcate, broader branch bearing large, slightly pointed, glandular disc; sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; unpigmented. Euspermatozoa 136 μ m; paraspermatozoa (Figure 3B, C) round to slightly oval, maximum diameter 21–26 μ m, packed with minute indistinct granules, one or two oval to elongate rod-pieces 4–17 μ m long. Pallial oviduct (Figure 4C) with spiral section of 5.5–6.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) is two whorls; bursa long, opening near anterior end of straight section of pallial oviduct, extending back to spiral section. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

Radula (Figure 8A–E): Relative radular length 0.87–1.68. Rachidian: length/width 1.04–1.29; cusps extremely variable: one large rounded cusp with two pointed denticles on either side (Figure 8E), or five pointed cusps decreasing in size on either side of central cusp (Figure 8A), or central cusp may be short and blunt (Figure 8C); hood generally well developed, sometimes narrow. Lateral: four to six cusps, largest central cusp variable in shape and size (rounded, pointed or short and blunt); two to three small pointed cusps on inside and one to two on outside of main cusp. Inner marginal: three to four cusps, largest central cusp variable in shape and size (rounded, pointed or short and blunt); one to two small pointed cusps on inside and one on outside of main cusp. Outer marginal: two short broad cusps, either may be slightly larger, both bluntly rounded or pointed. Cusps of all teeth more elongate in smallest specimen examined (6.9 mm shell height), and three (not two) cusps on outer marginal.

Material examined: 40 lots; one protoconch; nine penes; four sperm samples; three pallial oviducts; seven radulae.

Habitat: At low levels on trunks and roots of mangroves,



only rarely on leaves, up to 2.1 m above ground; common from seaward edge to landward fringe (personal observation, Costa Rica); also on stones, logs, and grass among mangroves; muddy rocks on sheltered shores (Contreras & Cantera, 1978; Guerrini, 1990; personal observation). Remains at or below water level at high tide (Contreras & Cantera, 1978; Borjesson & Szelistowski, 1989).

Range (Figure 6B): Specimens seen from El Triunfo, El Salvador (13°34'N; USNM; also Hernandez, 1979, from 13°14'N) to Paita, Peru (5°11'S; USNM). The southern limit in Peru requires confirmation; Peña (1970, 1971b) records the species from Puerto Pizarro (3°34'S). Nevertheless, there is a relictual stand of mangroves at San Pedro (5°30'S), near Paita; although this species was not recorded in a survey of this site by Peña & Vásquez (1985), occurrence there may be possible, perhaps only during El Niño events when warm equatorial water extends this far south.

Remarks: Of the three large, common *L. (Littoraria)* species found in the mangroves of western Central America, *L. varia* occurs at the lowest levels on the trees (although there is considerable overlap among them), and is the only one that is regularly submerged by the rising tide (Peña, 1971a; Contreras & Cantera, 1978; Borjesson & Szelistowski, 1989; Blanco et al., 1995). In comparison with the higher-zoned *L. variegata*, the shell is thicker and the aperture more narrow. This makes it less susceptible to predators that forage during high tide, such as puffer fish, portunid and xanthid crabs, as shown by field tethering and laboratory predation trials (Borjesson & Szelistowski, 1989). The shells are nevertheless frequently damaged during unsuccessful predation attempts, and most specimens bear the evidence in the form of one or more scars of repaired breakages.

The intraspecific variation in the form of the radular tooth cusps is extreme. Radular variation has been described in other littorinid genera (e.g., *Bembicium* by Reid, 1988; *Littorina* by Reid, 1996), but *L. varia* is the most striking example. Although only seven radulae were examined, variation was evidently not correlated with sex, adult size, or locality. All specimens were from mangroves, so there was no obvious correlation with microhabitat (cf. *L. pintado pullata* described earlier). There

may, however, be ontogenetic change in radular form; cusps of all teeth were relatively longest (although not as pointed as in one adult), and on the outer marginal more numerous, in the smallest (6.9 mm) specimen available; similar trends have been documented in *Littorina* (Reid, 1996; see also description of *L. zebra*). As in other studies of radular variation in littorinids, it is notable that tooth cusps vary together in the same way; in particular the major cusp on each of the five central teeth of each row are always similar in shape, suggesting a developmental constraint.

There is a possibility of confusion among *L. varia*, *L. zebra*, and *L. variegata*, which are sympatric over much of their range (although *L. variegata* alone occurs in Mexico). *Littoraria varia* is easily recognized by the smaller apical angle of its more elongate shell, its pure white columella and interior of the aperture, sculpture of strong spiral ribs, the largest of which marks the angled periphery. *Littoraria zebra* is likewise thick-walled, but has a broader shell, distinctly angled at the shoulder, with bright coppery orange columella and inner apertural margin, and striking broad brown stripes on the final whorl. *Littoraria variegata* is thinner in texture, has rounded whorls, columella edged with brown, and a variable shell pattern (usually of narrow oblique stripes, zigzags, or spiral lines). Penial shapes are diagnostic of each. The copulatory bursa is similar in all three, but the spiral part of the pallial oviduct shows most numerous whorls in *L. variegata* and fewest in *L. varia*.

Littoraria (Littoraria) zebra (Donovan, 1825)

(Figures 2H, I, 3D, 4E, 6C, 7D–G, 8F–H)

Turbo zebra Donovan, 1825: pl. 130; caption to pl. 131 (Panama; lectotype (here designated) Donovan, 1825: pl. 130).

Littorina zebra—Morrison, 1946: 9. Keen, 1958: 282; fig. 179. Keen, 1971: 366; fig. 189. Guerrini, 1990: 14.

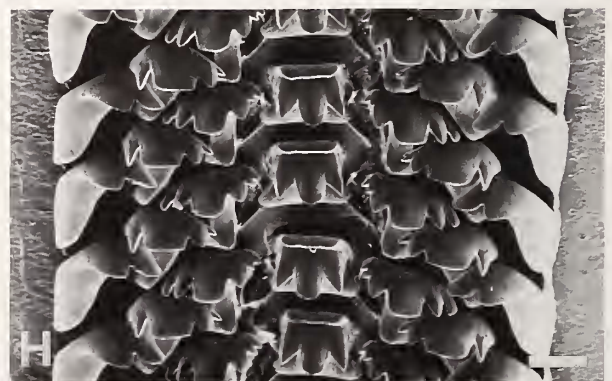
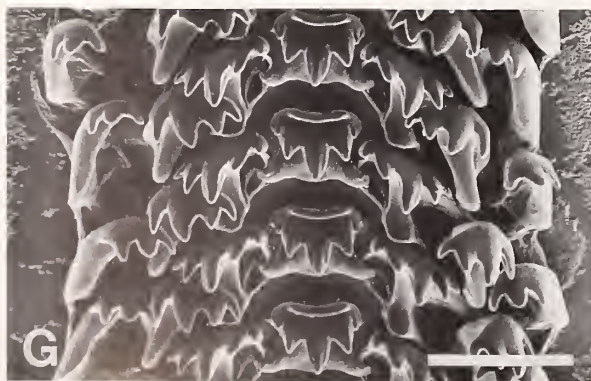
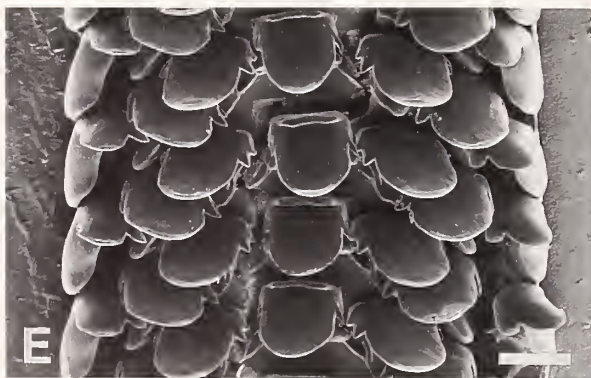
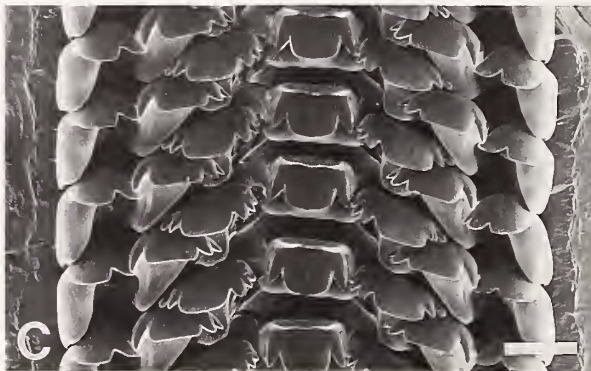
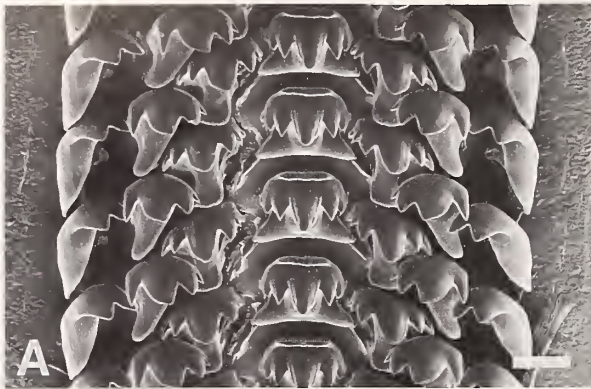
Littorina (Littoraria) zebra—Rosewater, 1970: 423; pl. 326, figs 6, 7.

Littoraria (Littoraria) zebra—Reid, 1986: 72; figs 41 (penis), 18 (cladogram), 99g. Reid, 1989: 97; pl. 2, fig. 2a; figs 7e (penis), 10c (oviduct), 14e (radula).

Littorina pulchra "Swainson" G. B. Sowerby, 1832: part 37; pl. 211, figs 2, 3 (no locality; types lost). Deshayes

Figure 7

Shells of *Littoraria varia* (A–C), *L. zebra* (D–G), *L. variegata* (H–K) and possible hybrids (L–N). A. Guayaquil, Ecuador (BMNH 1996200, Cuming Colln; note repaired crab breakage on penultimate whorl). B, C. Panama (BMNH 1967698, Cuming Colln). D. Puntarenas, Costa Rica (BMNH 1996201). E. Panama (BMNH 1996202). F, G. Panama (BMNH 1996203). H. El Salvador (BMNH 1996204; note eroded area where males attach in copulation position). I. Tumbes, Peru (BMNH 1996205). J. Lectotype of *Littorina variegata* Souleyet, in Eyedoux & Souleyet, 1852 (MNHN unregistered); La Puna, Guayaquil River, Ecuador. K. Tumbes, Peru (BMNH 1996206). L. Possible hybrid between *L. varia* and *L. variegata*; Puntarenas, Costa Rica (BMNH 1996154). M, N. Possible hybrids between *L. zebra* and *L. varia*; 2 miles west of Venado Beach, Veracruz, Panama (USNM 743087). Scale bar = 10 mm.



& Milne Edwards, 1843: 208. Adams, 1852: 399–400. Reeve, 1857: *Littorina* sp. 17: pl. 3, fig. 17a, b. Mörch, 1860: 68–69. Dall, 1909: 231. Pilsbry & Lowe, 1932: 124.

Littorina pulchra—Griffith & Pidgeon, 1834: 598; pl. 1, fig. 3.

Littorina pulchra—Philippi, 1846b: 2: 99; *Littorina* pl. 1, fig. 1. Weinkauff, 1882: 49–50; pl. 6, figs 6, 7.

Littorina (Melaraphie) pulchra—H. & A. Adams, 1854: 314. Tryon, 1887: 246; pl. 43, fig. 47.

Littorina (Littorinopsis) pulchra—von Martens, 1900: 581.

Littorina fasciata Gray, 1839: 139 (Pacific Ocean?; holotype BMNH 1968361, seen).

Taxonomic history: Until the resurrection of the earlier name by Keen (1958), this species was known by the name *pulchra*. The epithet *Littorina fasciata* Gray, 1839, has hitherto been incorrectly applied to the species here identified as *Littoraria variegata*. However, the synonymy with *L. zebra* is clearly indicated by Gray's description of "oblique transverse brown bands," "apex . . . purplish" and "whorls . . . concavely impressed near the suture"; furthermore, although this description was not accompanied by an illustration, the holotype in BMNH confirms the identification.

Diagnosis: Shell thick-walled; whorls shouldered; sculpture of fine spiral ribs; color orange with oblique brown stripes, aperture and columella orange. Penis with small filament, very large glandular disc on branch of blackish base.

Shell (Figure 7D–G): Mature shell height 16–40.6 mm. Shape turbinate ($H/B = 1.07$ – 1.29 , $SH = 1.28$ – 1.45); spire whorls rounded, sutures distinct; periphery of last whorl rounded, not angled; conspicuous angulation on shoulder of last whorl, resulting in square profile and flattened or concave area between shoulder and suture; thick-walled. Mature lip not flared, considerably thickened within; columella very broad (to 8 mm) and hollowed. Sculpture of numerous fine spiral ribs (36–44 on last whorl), evenly sized and separated only by incised lines; axial growth lines distinct, often giving ribs a minutely beaded appearance; fine spiral microstriae over whole surface if well preserved; periostracum not evident. Protoconch not clearly seen. Color coppery orange-brown, fading to cream, with striking pattern of broad chocolate brown stripes, forming oblique axial bands (7–12 at suture of last whorl) and zigzags, which tend to become spiral lines toward end of last whorl; spire whorls some-

times with a tessellated or reticulate pattern; apical two whorls of teleoconch purplish brown. Columella and aperture coppery orange; apertural margin marked with dark brown spots of external pattern.

Animal: Head, tentacles and sides of foot black, usually paler or unpigmented behind eye and at inside of tentacle base. Opercular ratio 0.36–0.40. Hypobranchial gland large, up to 1.5 mm wide in shell of 27.0 mm. Penis (Figure 2H, I) with wrinkled base and small smooth filament (20–30% total length); base bifurcate, bearing large, almost circular, glandular disc; sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; filament unpigmented, base black, glandular disc grey. Euspermatozoa 195–200 μm ; paraspermatozoa (Figure 3D) round to oval, maximum diameter 19–26 μm , packed with minute granules, one (rarely two to three) rectangular to oval rod-piece 5–18 μm . Pallial oviduct (Figure 4E) with spiral section of 7.5–8.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) is three whorls; bursa long, opening behind anterior end of straight section of pallial oviduct, extending back almost to spiral section. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

Radula (Figure 8F–H): Relative radular length 1.16–2.02. Rachidian: length/width 0.97–1.32; cusps variable, central cusp largest, pointed to bluntly rounded, one pointed cusp and a denticle on either side; hood well developed. Lateral: five to six cusps, largest central cusp short and blunt, or rounded or pointed; two to three small pointed cusps on inside and two on outside of main cusp. Inner marginal: four cusps, largest central cusp short, broad and blunt, or longer and pointed; two smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: two to four bluntly rounded cusps, outermost usually largest. All cusps relatively longest and most pointed in smallest specimen examined (shell height 8.2 mm).

Material examined: 28 lots; 14 penes; three sperm samples; six pallial oviducts; five radulae.

Habitat: On trunks and roots of mangroves, up to 2.0 m above ground; more common in middle zone of *Rhizophora* forest and landward fringe (personal observation, Costa Rica). Also on rocks, logs, and driftwood among

←

Figure 8

Radulae of *Littoraria varia* (A–E) and *L. zebra* (F–H). A. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; at 45°; shell H = 25.2 mm). B–D. Puntarenas, Costa Rica (BMNH 1996219; three views of radula, flat, at 45° and at 45° from side; shell H = 30.2 mm). E. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996213; at 45°; shell H = 19.1 mm). F, H. Golfito, Costa Rica (BMNH 1996214; two views of radula, flat and at 45°; shell H = 27.0 mm). G. Golfito, Costa Rica (BMNH 1996214; at 45°; shell H = 8.2 mm; juvenile). Scale bars = 50 μm .

mangroves (Contreras & Cantera, 1978; Guerrini, 1990; personal observation). In Colombia, Contreras & Cantera (1978) reported that *L. zebra* avoids submersion by the high tide, and during low tide remains in the branches of the trees, overlapping with and above the zone occupied by *L. variegata*. In a study at Buenaventura Bay, Colombia, the mean tidal level of *L. zebra* was slightly above that of *L. variegata*, but the vertical ranges of each were almost the same (Blanco et al., 1995). At two sites in Costa Rica, there was also considerable overlap between these two species, but *L. variegata* attained higher levels (personal observation).

Range (Figure 6C): Specimens have been seen from between Playa Tamarindo, Costa Rica (10°19'N, BMNH) and San Lorenzo, Ecuador (1°17'N, USNM); literature records extend the range northward to Santa Elena Bay, Costa Rica (10°59'N; Pilsbry & Lowe, 1932) and southward to Bahía de Caráquez, Ecuador (0°38'S; Guerrini, 1990). Not reported from El Salvador by Zilch (1954).

Remarks: This spectacular species is the type of the genus *Littoraria*. For comparison with similar species, see Remarks on *L. varia*. Together with *L. variegata*, this species is gathered for food in Colombia, and is of potential economic importance (Cantera & Contreras, 1978).

As mentioned above, there is uncertainty about the relative vertical zonation of the two species *L. zebra* and *L. variegata*. In assemblages of *Littoraria* species on mangrove trees elsewhere in the tropics, the shells of species occupying lower tidal levels on the trees are more thick-walled, which has been related to the requirement for protection from crabs and other crushing predators that forage at lower levels (Reid, 1984, 1986, 1992; Cook et al., 1985; Borjesson & Szelistowski, 1989). It is therefore surprising that the shell of *L. zebra* appears considerably thicker and stronger than that of *L. variegata*, with which it shares a similar zonation. However, zonation levels are generally observed during diurnal low tide. In an Australian study, *Littoraria* species have been shown to be highly mobile, moving vertically on the trees with the rise and fall of the tide, particularly at night and dawn, and their zonation may also be influenced by rainfall and spawning (Reid, 1984). Prolonged observation is therefore necessary to establish relative patterns of zonation, and to discover whether species are exposed to predators. Interestingly, *L. zebra* seldom shows the scars of unsuccessful predation attempts on its shell, which are so common in *L. varia* (zoned at the lowest level on the trees).

Littoraria (Littoraria) variegata (Souleyet, in Eydoux & Souleyet, 1852)

(Figures 2D, E, L, 3E, F, 4D, 5F–H, 6D, 7H–K)

Turbo bicarinatus Wood, 1828: 20; pl. 6, *Turbo* fig. 47 (types lost; not Sowerby, 1825).

Littorina bicarinata—Mörch, 1860: 69.

Littorina fasciata—Philippi, 1847: 2: 221; *Littorina* pl. 5, figs 1, 2 (not *Littorina fasciata* Gray, 1839 = *Littoraria zebra*). Weinkauff, 1878: 40; pl. 4, fig. 11 (not Gray, 1839).

Littorina fasciata—Adams, 1852: 397 (not Gray, 1839). Reeve, 1857: *Littorina* sp. 20; pl. 4, fig. 20; pl. 18, fig. 103a, b (not Gray, 1839). Morrison, 1946: 9 (not Gray, 1839). Keen, 1958: 282; fig. 176 (not Gray, 1839). Keen, 1971: 366; fig. 182 (not Gray, 1839). Peña, 1971b: 47 (not Gray, 1839). Guerrini, 1990: 14 (not Gray, 1839).

Littorina (Melaraphe) fasciata—H. & A. Adams, 1854: 314 (not Gray, 1839).

Littorina (Littorinopsis) fasciata—von Martens, 1900: 580–581 (not Gray, 1839). Rosewater, 1970: 423 (not Gray, 1839). Abbott, 1974: 69 (in part, fig. is *Littoraria varia*; not Gray, 1839). Alamo & Valdivieso, 1987: 25 (not Gray, 1839).

Littorina (Algaroda) fasciata—Zilch, 1954: 80–81; pl. 3, fig. 7 (not Gray, 1839).

Littoraria (Littoraria) fasciata—Reid, 1986: 72; figs 4n (penis), 18 (cladogram) (not Gray, 1839). Reid, 1989: 96 (not Gray, 1839).

Littorina variegata Souleyet, in Eydoux & Souleyet, 1852: 560; atlas pl. 31, figs 40–42 (la Puna, dans la rivière de Guayaquil [Ecuador]; lectotype (here designated, 25.9 mm; Figure 7J) + 1 paralectotype + 3 alcohol paralectotypes, MNHNP, seen).

Littorina (Melaraphe) varia—Tryon, 1887: 246; pl. 43, figs 45, 46 (in part, includes *Littoraria varia*; not Sowerby, 1832).

Littorina varia—Dall, 1909: 231, 285 (in part, includes *Littoraria varia*; not Sowerby, 1832).

Taxonomic history: Apparently following an initial misidentification by Philippi (1847), this species has been almost universally known by the name *L. fasciata*. However, *Littorina fasciata* Gray, 1839, is in fact a synonym of *L. zebra* (see Remarks on that species). The only available name for the present species is *L. variegata*. It is regrettable that this unavoidable name change, introduced here, may lead to confusion with *L. varia*.

Diagnosis: Shell of moderate thickness; whorls rounded; sculpture of fine spiral ribs; color cream variously patterned with brown flecks or stripes, aperture cream, edge of columella brown. Penis with unbranched, lightly pigmented base, incorporating glandular disc.

Shell (Figure 7H–K): Mature shell height 15–40.4 mm. Shape turbate (H/B = 1.14–1.44, SH = 1.35–1.53); spire whorls rounded, sutures distinct, not channelled; periphery of last whorl rounded, not angled, but sometimes marked by slightly enlarged rib; of moderate thickness. Mature lip not flared, thickened within as an indistinct rib; columella broad and hollowed. Sculpture of numerous fine spiral ribs, about 20 on last whorl, with three to five smaller riblets of varying size closely packed in the spaces between; axial growth lines often indistinct, but sometimes give ribs a finely beaded appearance; fine spiral microstriae over whole surface if well preserved; thin,

adherent periostracum. Protoconch 0.31 mm diameter, about three whorls, terminated by sinusigera rib, sculpture not preserved. Color whitish to cream or ochre, variously patterned with dark brown: fine flecks or dashes, sometimes merging into narrow spiral lines, but usually axially aligned to give 9–17 continuous oblique stripes, sometimes zigzags or coarse tessellation; pattern sometimes faint or absent. Edge of columella pale to dark brown, pillar cream; aperture cream to pale brown, pattern often showing through; apertural margin marked with dark brown spots of external pattern.

Animal: Head and tentacles dark grey, large unpigmented patch on inside of tentacle base, unpigmented stripe behind eye (Figure 2L); sides of foot flecked and lined with dark grey. Opercular ratio 0.43–0.47. Hypobranchial gland normal, up to 0.5 mm wide in shell of 20.3 mm. Penis (Figure 2D, E) with large, wrinkled base and small smooth filament (25–40% total length); base not bifurcate, bearing small, narrow, glandular disc distally; sperm groove open (also anterior vas deferens from prostate), extending to tip of filament; filament and glandular disc unpigmented, base with grey to blackish pigment in wrinkles, becoming darker basally. Euspermatozoa 255 μ m; paraspermatozoa (Figure 3E, F) round to elongate oval, maximum diameter 15–34 μ m, packed with small granules, one (rarely two) rectangular to elongate rod-piece extending full length of cell. Pallial oviduct (Figure 4D) with spiral section of 8.5–9.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) is three whorls; bursa long, opening behind anterior end of straight section of pallial oviduct, extending back to spiral section. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

Radula (Figure 5F–H): Relative radular length 1.41–2.14. Rachidian: length/width 1.07–1.31; cusps variable, central cusp largest, short and blunt, or rounded, one pointed cusp and usually a denticle on either side; hood generally well developed, sometimes narrow. Lateral: four to six cusps, largest central cusp short, broad and blunt; two to three small blunt or pointed cusps on inside and one to two on outside of main cusp; anterior face of tooth may be concave behind main cusp, so that inner and outer cusps are not aligned in same plane (Figure 5G). Inner marginal: four cusps, largest central cusp short, broad, and blunt; two small pointed cusps on inside and one on outside of main cusp. Outer marginal: two broad, bluntly rounded cusps, sometimes with small additional pointed cusp on outside.

Material examined: 56 lots; one protoconch; six penes; four sperm samples; five pallial oviducts; five radulae.

Habitat: On trunks, roots, and branches of mangroves, up to 2.5 m above ground; common throughout *Rhizophora* forest, from seaward edge to landward fringe (per-

sonal observation, Costa Rica). Sometimes also on muddy rocks on sheltered shores. This species climbs to avoid submersion by the high tide (Contreras & Cantera, 1978; Borjesson & Szelistowski, 1989). At two sites in Costa Rica it showed considerable overlap with *L. zebra* on the trees, but extended to higher levels (personal observation), although the reverse has been reported in Colombia (Contreras & Cantera, 1978; Blanco et al., 1995).

Range (Figure 6D): As first recorded by Carpenter (1857a) this species has a wide distribution. The known northern limits are Laguna Ojo de Liebre on the western coast of Baja California (27°45'N, USNM), La Paz (24°10'N, Pillsbury & Lowe, 1932) and Topolobampo in the Gulf of California (25°36'N, BMNH). Between Nayarit and El Salvador there is a gap of over 2000 km with no records, where the coastline is mainly of exposed rock and sand; here mangroves are largely restricted to enclosed brackish lagoons, in which *Littoraria* species are not known to occur (e.g., Stuardo & Villarroel, 1976). The southernmost record is from Puerto Pizarro, Tumbes, Peru (3°34'S; Peña, 1970, 1971b).

Remarks: This species is zoned at higher levels than *L. varia*, and unlike that species climbs to avoid submersion; correspondingly, its thinner shell is more susceptible to crushing by the predatory crabs and fish that forage in the mangroves during high tide (Borjesson & Szelistowski, 1989). Large female shells often show a smooth eroded patch on the penultimate whorl, presumably rasped by the radulae of males attached in this position during copulation. Although the shell is highly variable in coloration in the species as a whole, large samples from single localities show limited variability and cannot be described as polymorphic (a term strictly applied to discrete variation). Growth and allometry have been described by Cruz (1989), who detected no sexual dimorphism in size. For comparison with similar species, see Remarks on *L. varia*.

Possible hybrids of *Littoraria* species

(Figure 7L–N)

About 1300 shells of *L. varia*, *L. zebra*, and *L. variegata* have been examined during the present study, and almost all have been immediately identifiable because their shells are highly distinctive and show a narrow range of variability (at least in shape and sculpture). However, among them three specimens stand out, defying classification.

USNM 743087 (Figure 7M, N): The first two are present together with two typical *L. variegata* in a lot from “2 miles W of Venado Beach, Veracruz, Panama, NMNH-STRI Survey Stn 112, 5 Nov. 1972.” These two dry shells were first noted as possible hybrids in an annotation by J. Rosewater. Their dimensions are: H = 19.7 mm (H/B = 1.30; SH = 1.52); H = 22.7 mm (H/B = 1.30;

SH = 1.46). Both are thick-walled shells with internally thickened apertures indicating maturity. Superficially, shape and coloration resemble *L. variegata*; however, the shells are too solid and the spiral sculpture too coarse and regular. The sculpture is most like *L. zebra*, with closely spaced, minutely beaded, although somewhat irregularly sized spiral ribs; the broad columella is pale orange throughout (paler than in *L. zebra*, but not bordered with brown as in *L. variegata*). Internally, the apertural callus is white, a character found only in *L. varia*. In outline, the spire height is similar to that in *L. variegata*, but the last whorl is not uniformly rounded, but shows a slight angulation both at shoulder and periphery. External coloration is cream with a dark purplish brown pattern of coarse tessellation, aligned near the suture to form about 11 oblique stripes. It is tentatively suggested that these might be hybrids of *L. zebra* and *L. varia*.

BMNH 1996154 (Figure 7L): A third specimen was found together with typical forms of all three species in a *Rhizophora* forest at Puntarenas Yacht Club, Costa Rica (personal collection 5 December 1985). The shell outline is similar to the two shells described above (H = 25.4 mm; H/B = 1.32; SH = 1.45), but the texture is thinner and the lip not thickened. The sculpture is of numerous fine spiral ribs, but these are not crowded together or minutely beaded (as in *L. zebra*). Coloration is cream with a dark purplish brown pattern of small dashes, indistinctly aligned near the suture; the columellar pillar is white, the parietal callus and columellar edge ochraceous (as in *L. variegata*), and the internal callus of the aperture white (as in *L. varia*). The principal cusps of the five central teeth of the radula are short and blunt; there are three cusps on the outer marginal (not known in adult *L. varia*, but common in *L. variegata* and *L. zebra*). The head and sides of the foot are black; the hypobranchial gland is large (up to 1.9 mm wide); the ovary is not developed, but the pallial oviduct is well formed, with a spiral part of 6.5 whorls (of which the capsule glands occupy three). Unfortunately, the female reproductive tract is not as clearly diagnostic of species as the male, but the characters listed appear to combine, or are intermediate between, those of *L. varia* and *L. variegata*. Conceivably this specimen could be a hybrid between these two.

Remarks: In the absence of genetic evidence, this suggestion of hybridization must remain tentative. It is clear that these three specimens show combinations of characters that are sufficiently unusual that they are probably not simply aberrant examples of one or other of the three large mangrove-dwelling *Littoraria* species. Alternatively, they might represent an additional undescribed species. This seems less likely, for two reasons. The thickness, sculpture, and columellar color of the two collections are sufficiently different that it could be doubted that they are conspecific. Secondly, if one (or even two) ad-

ditional large *Littoraria* species were present in the mangroves of Costa Rica and Panama, it is improbable that it would be represented by so few specimens among the large collections available from these areas. However, the possibility cannot be dismissed, and further material should be sought. Hybrids between littorinid species have been claimed from morphological evidence only once before; this was the case of intermediates between *Nodilittorina australis* (Gray, 1826) and *N. nodosa* (Gray, 1839) reported by Rosewater (1970); these two are now known to belong to a single variable species (Reid, 1989). This explanation is quite clearly untenable in the present examples. Since the copulatory behavior of male littorinids is somewhat indiscriminate, interspecific copulation attempts have often been observed in the field (see Reid, 1986: 59–61 for *Littoraria* species; Reid, 1996: 14–15 for review in *Littorina* species). Attempts have been made to hybridize closely related *Littorina* species in the laboratory, but almost all have failed (Warwick et al., 1990; Boulding et al., 1993). The only successful example of laboratory hybridization so far reported was between *Littorina saxatilis* (Olivi, 1792) and *L. arcana* Hannaford Ellis, 1978, and even then no hybrids were detected in natural populations by allozyme electrophoresis (Warwick et al., 1990). If natural hybrids do occur, they are likely to be extremely rare. Conceivably, however, the case of the three large *Littoraria* species in the Eastern Pacific might provide a system in which rare natural hybrids could be more readily recognized. Most littorinid sister-species are so similar in shell morphology that natural hybrids are unlikely to be conspicuous in the field. The anatomical similarities of these three Eastern Pacific species suggest recent divergence (cladogram of Reid, 1989), and yet each has a highly distinctive shell morphology, so that large numbers of individuals can quickly be scanned for aberrant examples. Further anatomical and genetic investigation of this possibility would be of interest.

Littoraria (Littoraria) rosewateri Reid, sp. nov.

(Figures 3G, H, 6E, 9A–D, 10D, 11A–E, K, L)

Littorina debilis—Morrison, 1946: 9–10 (not Philippi, 1846, a synonym of *Nodilittorina ziczac* (Gmelin, 1791); based on USNM 588870, seen).

Littorina aberrans—Keen, 1971: 365; fig. 179 (in part; includes *Littoraria aberrans* (Philippi, 1846)).

Littorina scabra aberrans—Rosewater, 1980b: 158–162; figs 11, 12 (radula) (in part; other figs are *Littoraria aberrans* (Philippi, 1846)).

Littoraria (Littoraria) n. sp. Reid, 1986: 73; figs 4k (penis), 18 (cladogram).

Types: Holotype BMNH 1996155 (Figure 9B), 11 paratypes in alcohol BMNH 1996156, one paratype USNM 880187 (Figure 9A). Type locality: Topolobampo, 20 km west of Los Mochis, Sinaloa, Mexico.

Etymology: This species is named in memory of the late Joseph Rosewater, who had a special interest in the Littorinidae, and contributed much to the understanding of their systematics (see Rehder, 1986, for tribute and bibliography).

Taxonomic history: Hitherto, this species has generally been misidentified as *L. aberrans* (e.g., Keen, 1971) or included with it (Rosewater, 1980b). It was noted as an undescribed species by Reid (1986).

Diagnosis: Shell small, elongate, solid; last whorl rounded; protoconch 0.30 mm diameter. Penis with large filament containing closed sperm duct; glandular disc on branch of base. Pallial oviduct with capsule gland, indicating spawning of pelagic eggs.

Shell (Figure 9A–D, 10D): Mature shell height 5–12.3 mm. Shape elongate ($H/B = 1.70$ – 1.86 , $SH = 2.00$ – 2.44); spire whorls rounded, sutures distinct; last whorl uniformly rounded, sometimes a slightly enlarged rib at periphery; of moderate thickness. Mature lip not flared, but previous lips may be visible as strong growth interruptions near end of final whorl; columella narrow, not hollowed, pinched at base, with slight convex bulge above. Sculpture of incised spiral lines, five to eight visible on spire whorls (Figure 10D), increasing to 17–45 at end of last whorl; lines sometimes obsolete on last whorl; axial growth lines indistinct on spire whorls, but may become conspicuous on last whorl; surface shining, without spiral microstriae; periostracum thin, adherent. Protoconch (Figure 10D) 0.30–0.31 mm diameter, about three whorls, terminated by sinusigera rib, sculpture poorly preserved, but five to six spiral ribs visible. Color polymorphic; ground color cream to pale yellow brown, or pale pinkish orange; variable development of brown pattern; usually of smudged spots or dashes on ribs, aligned near suture and periphery to form short axial stripes or series (8–16 on last whorl), but pattern sometimes absent. Columella and parietal callus purplish brown in patterned shells, otherwise pale orange brown; aperture pale yellowish brown or pinkish orange, external pattern showing through.

Animal: Head grey to black, pale at tip of snout, tentacles pale with transverse grey lines; unpigmented patch at inside of tentacle base and behind eye; sides of foot pale grey or speckled with black (Figure 11A). Opercular ratio 0.45–0.46. Penis (Figure 11B–E) with wrinkled, bifurcate base bearing rectangular glandular disc; filament large (50% total length), constricted at base, tapering; sperm duct closed (also anterior vas deferens from prostate), opening at tip of filament; penis unpigmented, filament sometimes pale reddish orange in life. Euspermatozoa 62–72 μm ; paraspermatozoa (Figure 3G, H) round to oval, maximum diameter 10–14 μm ; packed with large spherical granules; single, narrow rod-pieces 18–24 μm , projecting from cells. Pallial oviduct (Figure 11K, L) with

spiral section of 3.5–4.5 whorls, of which capsule gland (with proximal opaque and distal translucent portion) about 1.5 whorls; bursa small, opening near anterior end of short straight section of pallial oviduct. Spawn and development not observed; presence of capsule gland suggests pelagic egg capsule; type of protoconch indicates planktotrophic development.

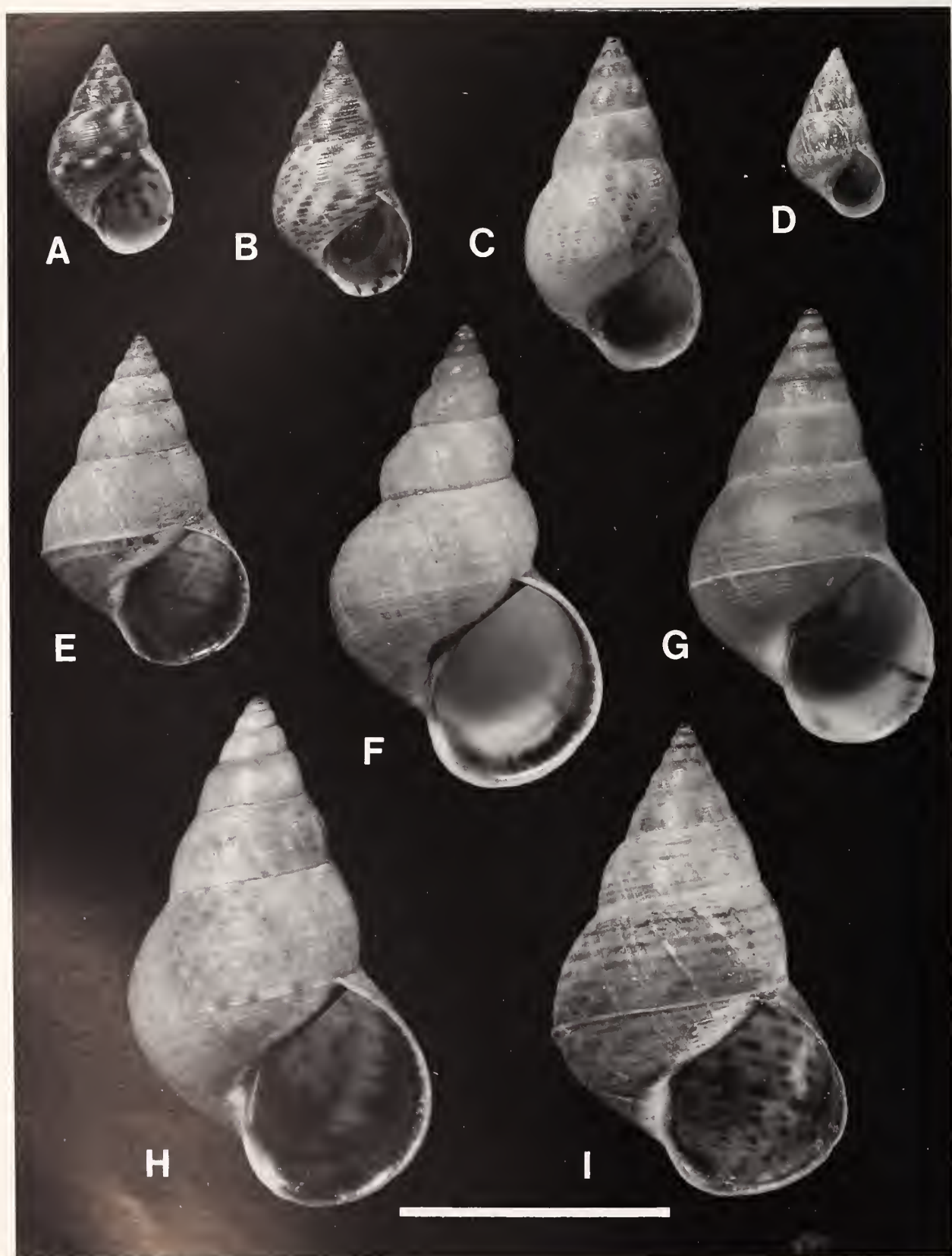
Radula (Figure 12A–E): Relative radular length 0.90–1.67. Rachidian: length/width 0.95–1.21; central cusp largest, usually pointed, sometimes bluntly rounded, one pointed cusp and usually a denticle on either side; hood well developed. Lateral: five to six cusps, largest central cusp pointed or bluntly rounded; two to three smaller pointed cusps on inside and one to two on outside of main cusp. Inner marginal: four cusps, largest central cusp pointed or rounded; two smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: four to six pointed cusps, outermost largest.

Material examined: Types; 19 lots; two protoconchs; seven penes; seven sperm samples; five pallial oviducts; six radulae.

Habitat: Abundant among grass and sedge tussocks in salt marshes; on and under boulders in littoral fringe on sheltered muddy shores; on leaves and branches of mangroves (*Avicennia*). Typically at edges of brackish lagoons, creeks, or near freshwater seepages on shore. Morrison (1946) reported it as extremely abundant on rotting coconut fronds, in drift behind the sand barrier at the mouth of a swamp.

Range (Figure 6E): This species has a wide range, although available records are few. On the west coast of Baja California it has been found at Bahía Magdalena (24.5°N, USNM), and frequently on the eastern shore of the Gulf of California, from Puerto Peñasco (29°59'N, LACM) to Topolobampo (25°36'N, BMNH). There is then an apparent gap of over 3000 km, where much of the coastline is of exposed sand and rock; there are, however, brackish lagoons with mangrove vegetation where the species might be found (although molluscan diversity is low in such habitats, e.g., Stuardo & Villarroel, 1976). There are several records from Costa Rica and Panama, and the most southerly record is from Puerto Pizarro, Peru (3°30'S, LACM).

Remarks: This species has probably often been overlooked because of its small size and unusual habitat at the highest tidal levels on shores and in salt marshes. When it has been collected, it has previously been confused with *L. aberrans*. The two are easily distinguished: *L. rosewateri* is smaller in size, more solid, the spire usually relatively taller, and the small protoconch is of the planktotrophic type (cf. large protoconch of few whorls indicating nonplanktotrophic development in *L. aberrans*); characters of the reproductive anatomy are diagnostic.



Subgenus *Bulimilittorina* Reid, 1989**Type species:** *Littorina aberrans* Philippi, 1846**Diagnosis:** Development nonplanktotrophic with intracapsular metamorphosis; penis bifurcate, base containing two long, coiled, glandular structures opening at pair of papillae; capsule gland absent in pallial oviduct; embryos brooded in mantle cavity, released as crawling young (diagnosis after Reid, 1989).*Littoraria (Bulimilittorina) aberrans* (Philippi, 1846)

(Figures 3I, 6F, 9E–I, 10A–C, E–G, 11F–J, 12F–H)

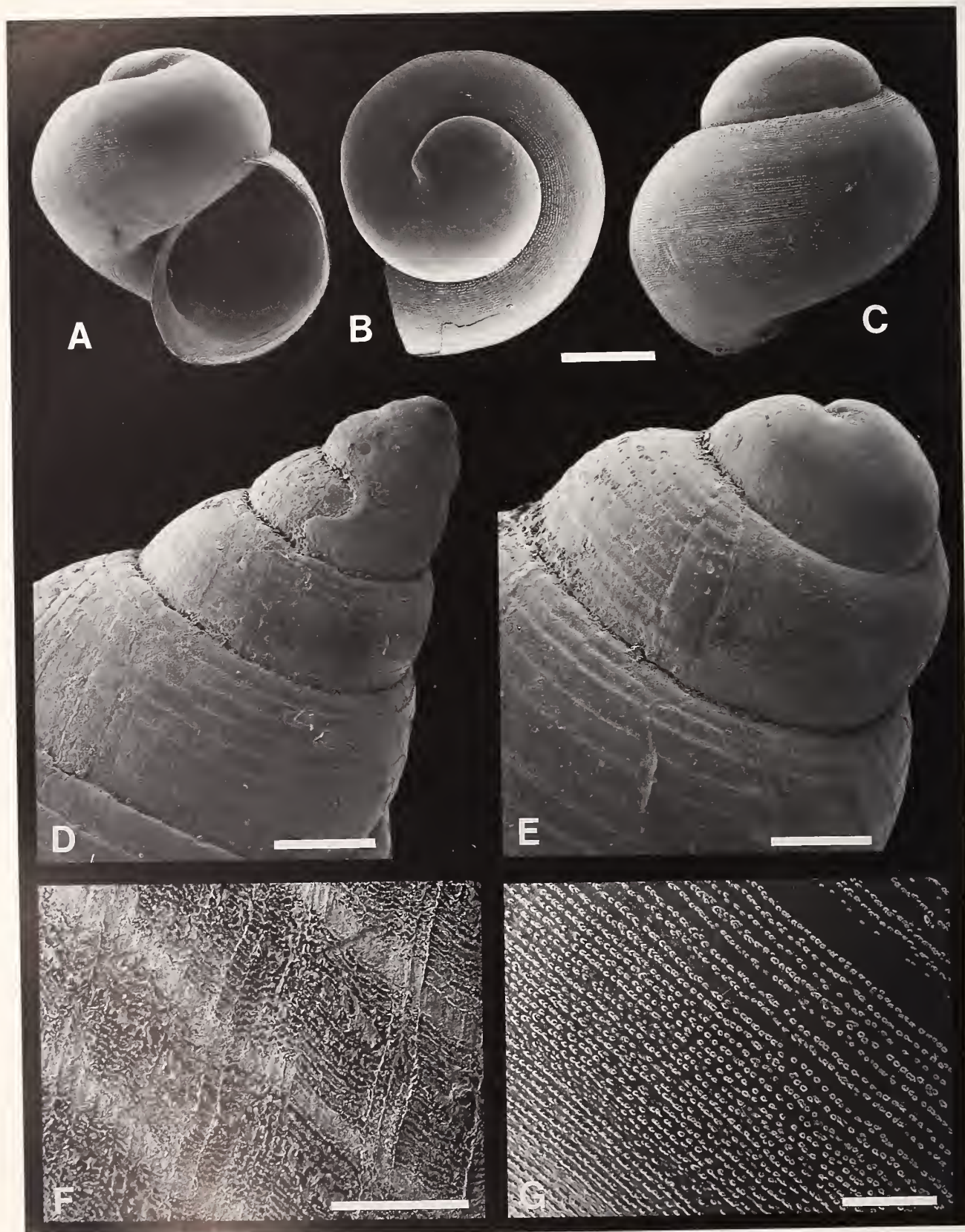
Littorina? *aberrans* Philippi, 1846a: 142–143 (Panama; holotype BMNH 1968325, seen; Figure 9F).*Littorina aberrans*—Philippi, 1847: 3: 11; *Littorina* pl. 6, fig. 9. Weinkauff, 1882: 72–73; pl. 9, fig. 13.*Littorina aberrans*—Reeve, 1857: *Littorina* sp. 59; pl. 12, fig. 59. von Martens, 1900: 587–588. Keen, 1971: 365 (in part; fig. is *Littoraria rosewateri*).*Littorina (Littorinopsis) scabra aberrans*—Rosewater, 1970: 423.*Littorina scabra aberrans*—Rosewater, 1980b: 158–162; figs 3, 6 (in part; other figs. are *Littoraria rosewateri*).*Littorina (Melaraphe) aberrans*—Tryon, 1887: 245; pl. 43, fig. 32.*Littoraria aberrans*—Reid, 1986: 14, 73, 77–79; fig. 18 (cladogram).*Littoraria (Bulimilittorina) aberrans*—Reid, 1989: 14, 28, 31, 38, 42, 85–86, 97–98; figs 7h (penis), 10f (oviduct), 14h (radula), 15 and 16 (cladograms).*?Littorina glabrata*—Morrison, 1946: 9 (not Philippi, 1846 = *Littoraria glabrata*).**Taxonomic history:** In the original description, Philippi (1846a) doubtfully referred this species to *Littorina*, remarking on the resemblance to the terrestrial pulmonate *Bulimus*, and this uncertainty persisted (Tryon, 1887; von Martens, 1900). Throughout the nineteenth century this species was known only from the holotype (Philippi, 1847; Reeve, 1857; Tryon 1887; von Martens, 1900), and since then *L. aberrans* has been figured only by Rosewater (1980b) and Reid (1989).**Diagnosis:** Shell elongate, delicate; last whorl sometimes

keeled at periphery; mature lip slightly flared; protoconch 0.68 mm diameter. Penis with large filament containing open sperm groove; base contains two large tubular glands, opening at two papillae on side branch. Pallial oviduct without capsule gland. Ovoviviparous; mantle cavity packed with embryos in brooding females.

Shell (Figure 9E–I, 10A–C, E–G): Mature shell height 9–18.7 mm; marked sexual dimorphism in size, largest male 12.0 mm. Shape high-conical (H/B = 1.58–1.76, SH = 1.87–2.15); spire whorls gently or well rounded, sutures distinct; periphery marked by sharp, keeled rib in juveniles, often becoming indistinct on last whorl which is then uniformly rounded; thin-shelled and delicate. Mature lip slightly flared, and if growth is resumed may occasionally remain as a single varix; columella a simple narrow pillar, slightly pinched at base, becoming detached in largest shells to give slight pseudoumbilicus. Sculpture of 8–11 weak incised spiral lines on spire whorls (Figure 10E); on last whorl developing into 21–33 weak, narrow, rounded ribs; peripheral rib is a sharp keel in juveniles and some adults; periostracum prominent for the genus; fine periostracal ridges (Figure 10F) appear at low magnification as microstriae over whole surface; axial growth lines marked by slight periostracal flanges; rarely, growth lines are prominent and numerous on last whorl, intersecting with spiral ribs to give indistinctly cancellate appearance. Protoconch (Figure 10A–C, E) 0.68 mm diameter, 1.8 whorls, terminated by straight growth line; first whorl smooth, then sculptured by numerous rows of minute (3 µm diameter) tubercles, developing first near suture (Figure 10G). Color polymorphic; ground color cream to pale brownish yellow; variable development of brown pattern: usually a rather regular checkered pattern of small dashes or spots on ribs, sometimes aligned in axial series (11–20 on last whorl), or uniformly finely mottled if spots are small, but pattern sometimes absent; color often varies with growth: brown at apex, pattern pale or absent on spire whorls, then darker on last whorl, and most intense just behind lip. Columella, parietal callus, and aperture near lip dark purplish brown in patterned shells, cream or pale brown in unpatterned shells.**Animal:** Head and tentacles dark grey to black, pale at tip of snout; tentacles indistinctly banded, unpigmented

Figure 9

Shells of *Littoraria rosewateri* Reid, sp. nov. (A–D) and *L. aberrans* (E–I). A, B. Paratype (A; USNM 880187) and holotype (B; BMNH 1996155) of *Littoraria rosewateri* Reid, sp. nov.; Topolobampo, 20 km west of Los Mochis, Sinaloa, Mexico. C. East end of causeway to Medanos Blancos, Sinaloa, Mexico (LACM 120157). D. Golfito, Costa Rica (BMNH 1996207). E. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996208). F. Holotype of *Littorina aberrans* Philippi, 1846 (BMNH 1968325); Panama. G. Farfan River, Panama (USNM 380676). H. Farfan Beach, Panama (USNM 380675). I. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996208). Scale bar = 10 mm.



patch at inside of tentacle base and sometimes behind eye (Figure 11F); sides of foot mottled with black. Opercular ratio 0.48–0.50. Penis (Figure 11G–I) with wrinkled, bifurcate base bearing two short papillae with blunt, puckered openings in place of glandular disc; two large, convoluted, tubular glands visible by transparency, extending from papillate openings to very base of penis; filament large (40–60% total length), tapering; open sperm groove (also anterior vas deferens from prostate), extending to tip of filament; penis largely unpigmented, base faintly grey. Euspermatozoa 120 μm ; paraspermatozoa (Figure 3I) round, 9–13 μm diameter, surface minutely rough, contents indistinctly granular, no obvious rod-pieces. Pallial oviduct (Figure 11J) with spiral section of 2.5–3.5 whorls, capsule gland absent; bursa short, opening near anterior end of long straight section of pallial oviduct. Development ovoviviparous, with intracapsular metamorphosis; in brooding females mantle cavity is solidly packed with embryos; one female (17.6 mm) contained 600 unencapsulated embryos, all at same stage of development, shell diameters 0.65–0.68 mm (Figure 10A–C). Gill leaflets similar in gross appearance to those in other members of genus; in a female of 15.0 mm, width of gills (from hypobranchial gland to osphradium) 4.0 mm, maximum height of leaflets 0.5 mm.

Radula (Figure 12F–H): Relative radular length 0.64–0.74. Rachidian: length/width 1.11–1.47; central cusp largest, with mucronate point, one pointed cusp and a denticle on either side; hood well developed. Lateral: seven cusps, largest central cusp square; four short pointed or rounded cusps on inside and two small pointed cusps on outside of main cusp; anterior face of tooth is concave behind main cusp, so that inner and outer cusps are not aligned in same plane. Inner marginal: five to seven cusps, largest blunt; three to five smaller pointed cusps on inside and one on outside of main cusp. Outer marginal: four to five cusps, outermost pointed, others bluntly rounded; neck and base of tooth unusually broad.

Material examined: Type; 12 lots; two protoconchs; 10 embryonic shells; five penes; two sperm samples; three pallial oviducts; four radulae.

Habitat: Leaves, branches and roots of *Rhizophora* at

landward edge of mangrove forests, up to 3.5 m above ground; apparently always scarce.

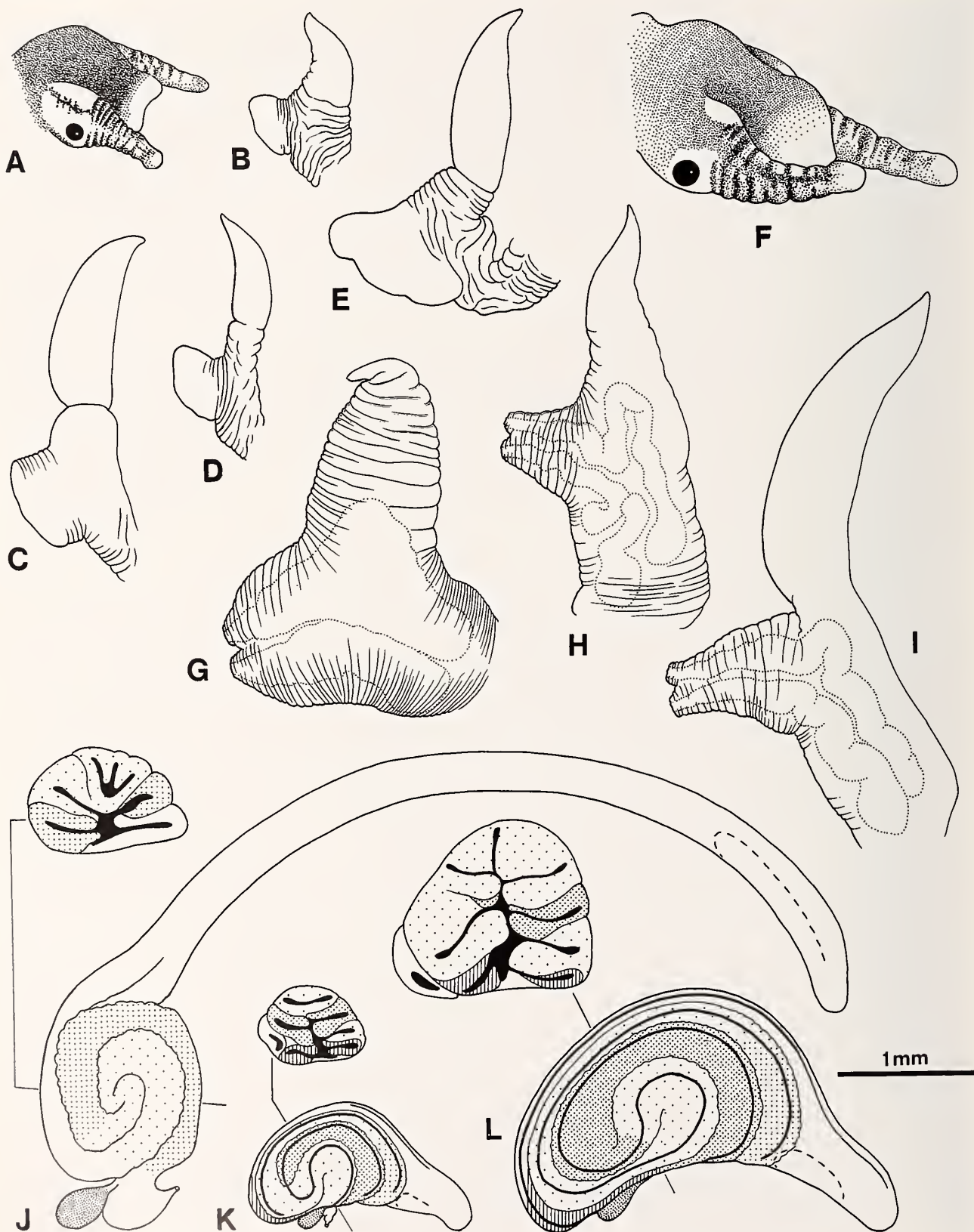
Range (Figure 6F): The few available records are from Playa Tamarindo (10°19'N, BMNH), Puntarenas, and Quepos, all in Costa Rica, and Farfan River, Taboga Island and San José Island (8°15'N, USNM), all in Panama. Since the species is uncommon and occurs at high tidal levels, it may have been overlooked elsewhere. "*Littorina scabra aberrans*," mentioned from the branches and foliage of mangroves in Colombia (Blanco et al., 1995), may refer to this species (or perhaps to *L. rosewateri*), but has been described as "very abundant" (Cantera et al., 1983).

Remarks: This species is the only member of the genus, and one of only four species in the family (Reid & Geller, 1997), to show ovoviviparity with intracapsular metamorphosis, so that crawling juveniles are released from the female. Twelve other species of *Littoraria* (the members of the subgenus *Littorinopsis*) are also ovoviviparous, but in these the larvae are released from the mantle cavity as planktotrophic early veligers with shells about 0.1 mm in diameter (Reid, 1986). Assuming that ovoviviparity has arisen only once in *Littoraria*, the condition in *L. aberrans* has presumably been derived from that shown by *Littorinopsis* species (Reid, 1989). Elimination of the marine larval stage is presumably adaptive in this species which inhabits such high levels in the trees, often at the landward fringe of mangrove forests where contact with the tide is infrequent, making it effectively a terrestrial snail. This type of development might be expected to be advantageous for other *Littoraria* species which occupy a similar high-level habitat elsewhere in the tropics; however, its absence may perhaps be explained by the consequent limitation of larval dispersal, which increases the likelihood of extinction (Reid & Geller, 1997). In immature or non-brooding females, ovoviviparous development is still recognizable because of the absence of capsule glands (and consequently small spiral section) in the pallial oviduct.

Another anatomical peculiarity of this species is the unique structure of the penis. All other species of the genus possess a glandular pad or sucker, the penial gland-

Figure 10

SEM details of shells of *Littoraria aberrans* (A–C, E–G) and *L. rosewateri* Reid, sp. nov. (D). A–C. Unencapsulated juveniles of *L. aberrans* from mantle cavity of brooding female; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). D. Apex and protoconch of *L. rosewateri* Reid, sp. nov.; Golfito, Costa Rica (BMNH 1996217). E. Apex and protoconch of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). F. Detail of sculpture and periostracum on last whorl of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). G. High-power detail of sculpture of larval shell of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). Scale bars: A–E = 200 μm ; F = 400 μm ; G = 50 μm .



dular disc (although this is not clearly differentiated in the basal species *L. pintado*). The tubular glands of *L. aberrans* are superficially similar to the mamilliform penial glands of other Littorininae, but their histology and staining reactions suggest that they are not homologous, and have probably been formed by infolding of the penial glandular disc (Reid, 1989).

The delicate shell of *L. aberrans*, with flared aperture, is similar to those of the members of the subgenus *Littorinopsis* that likewise inhabit high supratidal levels among the foliage of mangrove trees (Reid, 1986). A study of the behavior of this virtually terrestrial species would be interesting, for it is likely that it rarely comes into contact with the high tide (see Reid, 1984, for account of the behavior of Australian *Littoraria* species). Consequently it avoids the powerful predators such as fish and crabs that forage at lower levels on the trees during high tide, and a thick protective shell is unnecessary (Reid, 1992). The pigmentation of the shell is variable, and this is apparently a true polymorphism, since both unpigmented and variously patterned shells can be found together. However, none corresponding to the orange-pink morph of other polymorphic *Littoraria* species have yet been seen. Shell color polymorphism in *Littoraria* is associated with a habitat among the foliage of mangrove trees (Reid, 1986), and the color polymorphism of both *L. rosewateri* and *L. aberrans* strengthens this correlation. It is believed to be maintained by visual selection against the varied background, and may be adaptive in relation to predation (Cook, 1983, 1986, 1992; Hughes & Mather, 1986; Reid, 1987; Cook & Garbett, 1992).

This species is one of the rarest littorinids in museum collections. This is not simply the result of its limited geographical distribution, for it appears always to be genuinely scarce in its mangrove habitat. This is in contrast to the high abundance attained by some other foliage-dwelling *Littoraria* species (Reid, 1985). The holotype was for long the only specimen known; this shell (Figure 9F) is an aberrant example with exceptionally rounded

whorls, narrow spire, and fine spiral ribs. This partly explains the early doubt about its generic allocation (Philippi, 1846a; Tryon, 1887; von Martens, 1900), for this shell does closely resemble some terrestrial prosobranchs of the genus *Chondropoma* Pfeiffer, 1847. Nevertheless, the protoconch, sculpture of the early whorls, columella, and dark pigmentation around the aperture are sufficient to identify it with others of the species, and intermediates with rounded last whorls (Figure 9H) connect it with the more typical form with keeled periphery and less marked sutures (Figure 9E, G, I).

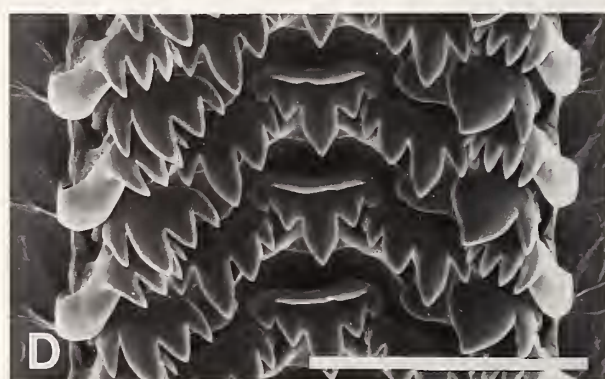
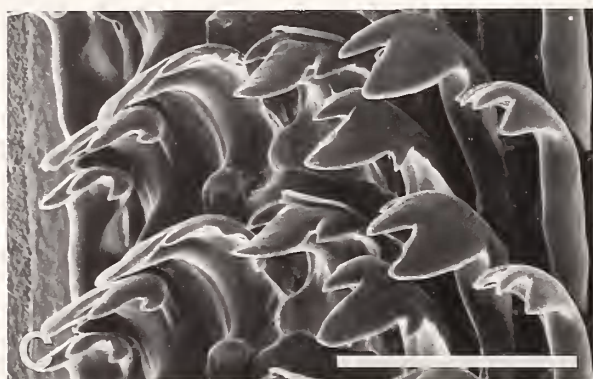
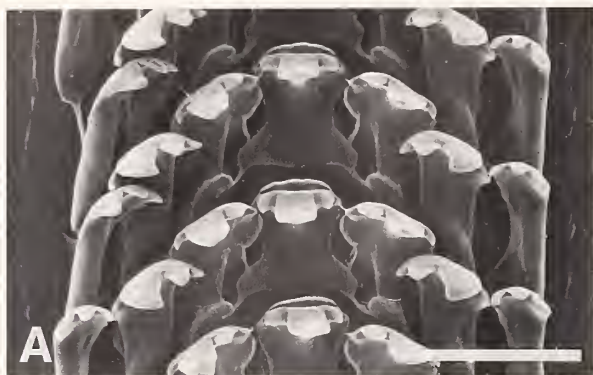
Among other *Littoraria* species in the Panamic province, confusion is only likely with *L. rosewateri* (see Remarks on that species). In the absence of accurate locality information, confusion could easily arise with *L. angulifera* (Lamarck, 1822) from the Caribbean coast of Central America. That species reaches larger size (36 mm), is generally a broader, more solid shell with more rounded whorls, and the columella, while narrow, is excavated; most importantly the sculpture is finer (50–90 ribs on last whorl, cf. 21–33 in *L. aberrans*), and the protoconch is of the planktotrophic type (0.35 mm diameter, about 3 whorls, sinusigera rib). Anatomically, the penis of *L. angulifera* has a bifurcate base bearing a glandular disc and a large filament (Reid, 1986: fig. 4o), and in the female the mantle cavity contains numerous small eggs and embryos that are brooded only to the early veliger stage with shells about 0.1 mm in diameter.

DISCUSSION

The evolutionary history of the marine species of Central America has long been of particular interest, because of the opportunity for the study of processes of speciation and extinction that is provided by the Pliocene emergence of the Isthmus of Panama (review by Vermeij, 1993). Until recently, it was believed that the formation of the land bridge about 3 million years ago not only isolated the Eastern Pacific and Western Atlantic provinces, but also caused an episode of extinction that was most severe in

Figure 11

Anatomy of *Littoraria rosewateri* Reid, sp. nov. (A–E, K, L) and *L. aberrans* (F–J). A. Head of *L. rosewateri* Reid, sp. nov.; Golfito, Costa Rica (BMNH 1996217). B–E. Penes of *L. rosewateri* Reid, sp. nov. B, D. Golfito, Costa Rica (BMNH 1996217; shell H of B = 5.1 mm; shell H of D = 4.7 mm). C. Penis of paratype of *L. rosewateri* Reid, sp. nov.; Topolobampo, Sinaloa, Mexico (BMNH 1996156). E. Río Marina Lagoon, San José Island, Pearl Islands, Panama (USNM 588870). F. Head of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218). G–I. Penes of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218; shell H of G = 12.0 mm; shell H of H = 9.1 mm; shell H of I = 9.7 mm; penis G is in a more contracted state than H and I; tubular glands visible by transparency are indicated by dotted outlines). J. Pallial oviduct of *L. aberrans*; Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218; shell H = 17.0 mm). K. Pallial oviduct of *L. rosewateri* Reid, sp. nov.; Golfito, Costa Rica (BMNH 1996217; shell H = 6.0 mm). L. Pallial oviduct of paratype of *L. rosewateri* Reid, sp. nov.; Topolobampo, Sinaloa, Mexico (BMNH 1996156; shell H = 9.3 mm). Shading conventions as in Figure 4.



the Atlantic, resulting in an impoverished Caribbean fauna (e.g., Vermeij & Petuch, 1986). It now appears that the extinctions began later, about 2.4 million years ago, perhaps as a result of changing patterns of upwelling and productivity (Jackson et al., 1993). Furthermore, extinctions were balanced by speciation and immigration, so that the overall diversity of Caribbean mollusks has not decreased since the Pliocene, and is not lower than that of the tropical Eastern Pacific (Allmon et al., 1993). The modern differences between the faunas of these two provinces are therefore the result not only of differential patterns of extinction, but also of origination. Unfortunately, neither the phylogenetic relationships nor fossil history of *Littoraria* are yet sufficiently well known to permit more than speculation on its evolutionary history in Central America.

The genus *Littoraria* has a pantropical distribution, and the oldest fossils occur in the Lower Eocene of France (Reid, 1989). Of the 36 Recent species, 25 occur in the Indo-West Pacific province. This compares with the six species reported here from the Eastern Pacific, five from the Western Atlantic and two from the Eastern Atlantic (Reid, 1986). The Western Atlantic species are *L. angulifera* (Lamarck, 1822), *L. flava* (King & Broderip, 1832), *L. irrorata* (Say, 1822), *L. nebulosa* (Lamarck, 1822), and *L. tessellata* (Philippi, 1847). On the basis of shell resemblance, Rosewater (1963) suggested the following pairs of "species analogues" on either side of the Isthmus of Panama: *L. varia* and *L. irrorata*, *L. pintado* and *L. tessellata*, *L. fasciata* and *L. angulifera*. However, shells are a poor guide to affinity among littorinids, and (with the possible exception of the first) none of these pairs is supported by anatomical evidence. Later, using both shell and radular characters, Rosewater (1980b) classified *L. scabra* (L.) as a single pantropical species, with subspecies *L. s. scabra* in the Indo-West Pacific, *L. s. angulifera* in the Atlantic, and *L. s. aberrans* in the Eastern Pacific, but again anatomical evidence has contradicted the implied relationships (Reid, 1986). In an early attempt to use biochemical characters to define "geminant species pairs" on either side of Panama, Jones (1972) analyzed allozyme frequencies and myoglobin banding patterns in 12 littorinids, but failed even to separate the generic groupings now recognized as *Littoraria* and *Nodilittorina*, much less to identify consistent species-pairs. Reid (1986) used a cla-

distic analysis of anatomical characters to define basal groups within *Littoraria*, and relied on subjective assessment of shell and penial form to suggest terminal groupings; on this basis the only close relationships of species across the Isthmus were among *L. varia*, *L. zebra*, *L. variegata*, and *L. irrorata*.

The present redescription of the *Littoraria* species of the Eastern Pacific has partly supported this earlier study. *Littoraria pintado* has no known sister-species among living members of *Littoraria*, and its subspecies, *L. p. pullata* is probably a relatively recent, Pleistocene, arrival in the Eastern Pacific from the west. The three species *L. varia*, *L. zebra*, and *L. variegata* are believed to form a clade, sharing likely synapomorphies of similar oviducts (tightly wound spiral; anterior bursa) and radulae (narrow posterior base of rachidian; only two to three cusps on outer marginal). This close relationship is also supported by the possible hybrids between them, discussed earlier. If they are indeed recently diverged from a common ancestor, their diversity of penial form is noteworthy, suggesting that the size of the glandular disc and degree of bifurcation of the base are readily modified, and might be species-recognition characters. Elsewhere in the genus, the same combination of radular and oviduct characters is found only in the Western Atlantic species *L. irrorata* (also exhibiting a non-bifurcate penis similar to that of *L. variegata*), which may therefore belong to the same clade. These four American species were linked by Reid (1986) with the Indo-West Pacific *L. vespacea* Reid, 1986, but reexamination of its radula has shown that it does not share the same characters. The new species *L. rosewateri* shares the synapomorphy of the closed penial vas deferens with the two Caribbean species *L. flava* and *L. tessellata* (these are likely sister-species, sharing a uniquely elongated penial filament, although the base is bifurcate only in the latter). Radular characters are also similar among these three, as is the overall form of the pallial oviduct. However, the bursa opens in an anterior position in *L. rosewateri*, posteriorly in *L. flava*, and is variable in position in *L. tessellata*; this character may not be phylogenetically informative in these species with a relatively short straight section of the pallial oviduct (as also suggested in *Littorina*, Reid, 1996: 349). The penial glands and intracapsular metamorphosis of *L. aberrans* are unique in the genus; its ovoviviparity is a synapo-

←

Figure 12

Radulae of *Littoraria rosewateri* Reid, sp. nov. (A–E) and *L. aberrans* (F–H). A–C. Radula of paratype of *L. rosewateri* Reid, sp. nov.; Topolobampo, Sinaloa, Mexico (BMNH 1996156; three views of radula, flat, at 45° and at 45° from side; shell H = 9.3 mm). D, E. Golfito, Costa Rica (BMNH 1996217; two views of radula, at 45° and flat; shell H = 6.0 mm; note aberrant inner marginal teeth on right side, with only two cusps). F–H. Punta Morales, Golfo de Nicoya, Costa Rica (BMNH 1996218; three views of radula, at 45°, flat and at 45° from side; shell H = 17.6 mm). Scale bars = 50 µm.

morphy shared with the subgenus *Littorinopsis*. No characters have yet been found which might indicate its relationships more precisely, and there is no reason to suppose that it is the sister-species of the Atlantic *L. (Littorinopsis) angulifera*. A reanalysis of the relationships of *Littoraria* species, using additional information on radular characters, is in progress.

The trans-Panamanian relationships discussed above are mostly different from those predicted from shell characters (Rosewater, 1963, 1980b). The lack of phylogenetically significant shell characters suggests that the fossil record may not be very helpful in reconstructing the evolutionary history of *Littoraria*. The pre-Pleistocene record of this genus in Central America is meager: two specimens of "*Littorina varia*" from the Pliocene of California (Hanna, 1926), three specimens of "*Littorina angulifera*" from the Miocene of Panama and Costa Rica (Woodring, 1957), and numerous records of *L. irrorata* from the Upper Miocene and Pliocene of Florida, North and South Carolina (e.g., Smith, 1936; Bequaert, 1943). These will be examined in future work.

During the emergence of the Panama land bridge, separation of Pacific and Atlantic populations of all marine species did not take place simultaneously. Those able to tolerate inshore conditions appear to have remained in genetic contact until the final stages of the imposition of the barrier (Knowlton et al., 1993), which is estimated to have occurred about 3.2 to 2.5 Ma (Coates et al., 1992). It is likely that the *Littoraria* species of mangrove environments, tolerant of turbidity and reduced salinity, were among the last to be separated. The absence of any obvious pairs of sister-species on either side of the modern isthmus is therefore surprising, and suggests that subsequent speciation, extinction, or migration may have obscured the expected pattern. It is also possible that there was already some differentiation of Pacific and Atlantic faunas before the isthmus appeared (Vermeij, 1993). For comparison, populations of *Littorina squalida* Broderip & Sowerby, 1829, in the Northern Pacific and Northern Atlantic were isolated about 4 to 2.4 Ma (as a result of climatic cooling following opening of the Bering Strait), and the resulting pair of sister-species, *L. squalida* and *L. littorea* (Linnaeus), are clearly recognizable on morphological grounds (Reid, 1996); this pair of planktotrophic developers has not undergone further speciation during this time. In contrast, the trans-Panamanian relationships discussed above suggest that some speciation may have occurred over a similar time scale, in these likewise planktotrophic *Littoraria* species (e.g., *L. varia*, *L. zebra*, *L. variegata* in the Eastern Pacific; *L. flava* and *L. tessellata* in the Caribbean). However, this remains to be investigated by further phylogenetic and paleontological work.

The geographical distributions of the Eastern Pacific *Littoraria* species clearly show limitation by habitat. *Littoraria pintado pullata* is restricted to oceanic high is-

lands (although current patterns may have prevented its colonization of the Galápagos Islands); on the American mainland it occurs commonly only at the extremity of Baja California. The remaining five species are all found predominantly among mangrove vegetation. The southern limits of three of these (*L. varia*, *L. variegata*, *L. rosewateri*) coincide with the southern limit of mangroves, in northern Peru, whereas that of *L. zebra* is a little farther north. Northern limits are less well established owing to a paucity of information about El Salvador and Guatemala, but the long stretch of coastline without coastal mangroves between southern Mexico and the Gulf of California appears to present a barrier to *L. varia* and *L. zebra*. Only *L. variegata* and *L. rosewateri* occur to the north of this barrier, thus showing markedly disjunct ranges. Although egg capsules have not yet been described, all these five species have planktotrophic development (indicated by protoconch and capsule glands), with the corresponding potential for wide larval dispersal. Rafting might also be a common means of dispersal in the mangrove-associated species. Only the sixth species, *L. aberrans*, has non-planktotrophic development, which might partly explain its restricted distribution.

Bequaert (1943) reported that the Caribbean species *L. angulifera* had reached the Pacific coast of Panama through the Panama Canal. However, this has not been confirmed by the extensive museum collections from this area examined during the present study. The record may perhaps have arisen from confusion with *L. aberrans*.

Among the mangrove-associated *Littoraria* species of the Indo-West Pacific, interspecific trends in shell architecture and coloration, at successive levels on the trees, have been explained as adaptive responses to gradients in crushing and visual predation; species zoned at lower levels are thick-shelled and monomorphic, those found at higher levels are thinner-shelled, and those inhabiting the foliage are thinnest, and often color polymorphic (see Introduction). As discussed in the Remarks on each species, these trends are also apparent in the Eastern Pacific, although *L. zebra* is somewhat anomalous.

The "hooded" type of rachidian tooth is found in most *Littoraria* species, including all those known to occur on trees, driftwood and marsh plants, which led to the suggestion that it might be adaptive for grazing on such substrates (Rosewater, 1980a; Reid, 1986, 1989). However, the new discovery that a small "hood"-like structure is also be present in some examples of the basal, rock-dwelling, species *L. pintado* suggests that it might perhaps be a synapomorphy of the genus, lost in a few species. Little is known about the diet of *Littoraria* species, but a mangrove-associated species (*L. angulifera*) and a salt-marsh species (*L. irrorata*) both include a significant component of fungal material in their diets (Kohlmeyer & Bebout, 1986; Newell & Bärlocher, 1993; Bärlocher & Newell, 1994). The intraspecific variation in form of the tooth cusps in *L. varia* (and to a lesser extent in *L. va-*

riegata and *L. pintado pullata*) is the most remarkable example in the family. Such extreme variation has not previously been found in *Littoraria* species (Reid, 1986), but has been reported in other littorinid genera (Reid, 1988, 1996; Padilla, 1998).

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